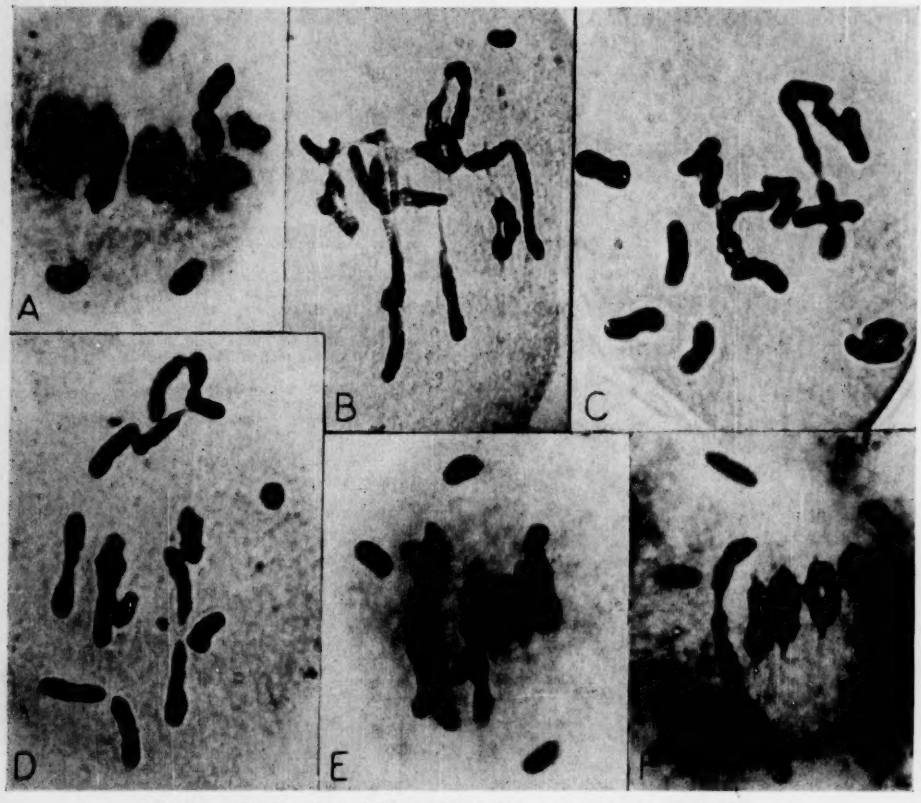
The Journal of HEREDITY



PERPLEXED CHROMOSOMES IN A BARLEY HYBRID

(SEE PAGE 125)

Hybrid Bermuda Grass — Glumeless Sweet Corn

Home-Brew Cells and Hybrid Corn in USSR

Snow-White and the Eight Fowl Genes

VOLUME 42 MAY-JUNE, 1951 NUMBER 3

The American Genetic Association

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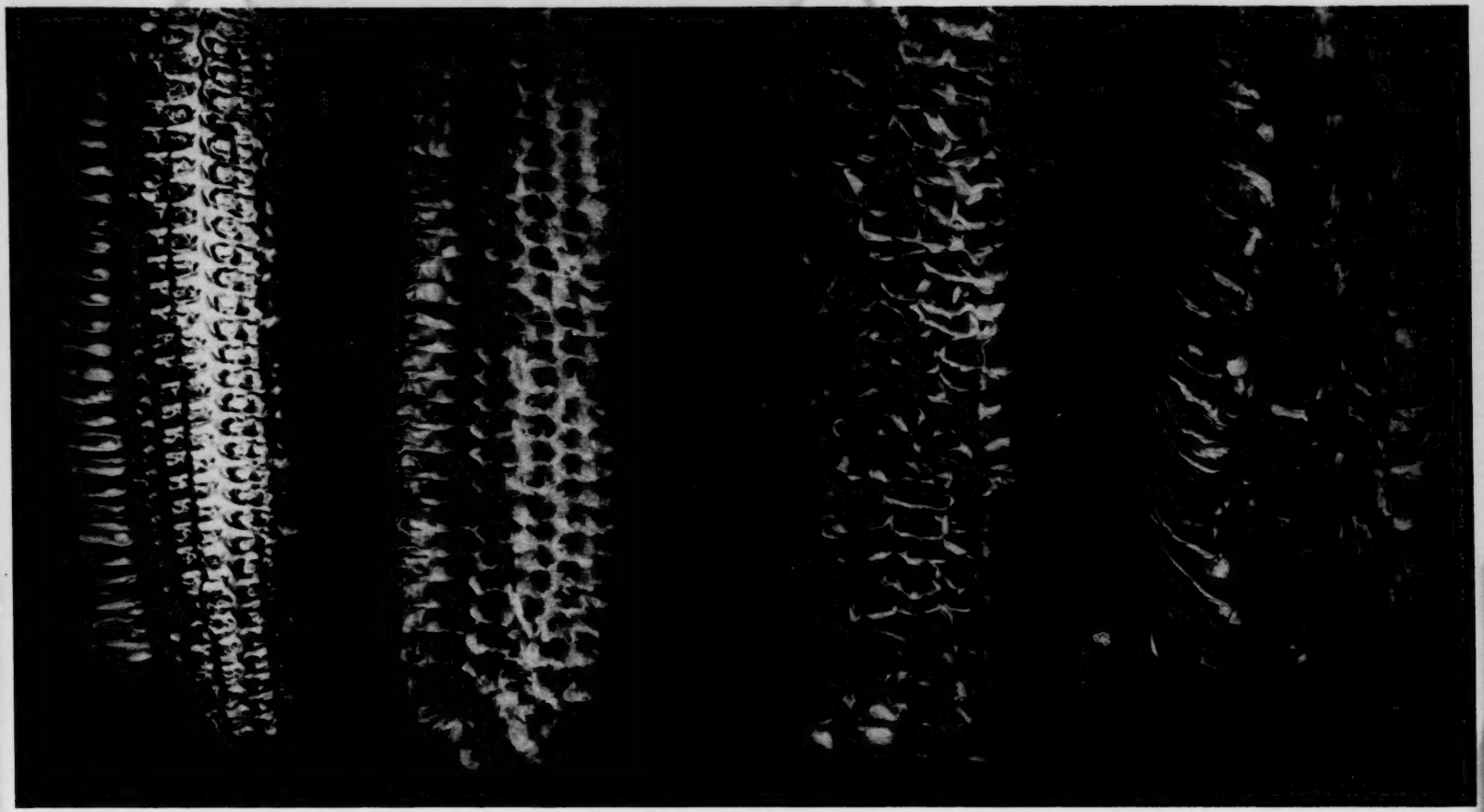

FROM NO-GLUMES TO PODS

Figure 1

The development of the glume in maize is conditioned by several genes. The dominant vestigial glume gene in its extreme expression inhibits the development of any glume (*A*), and also causes sterility of the male inflorescence. For comparison a normal ear of sweet corn (*vgvg*) is shown at *B*. Ears *C* and *D* show half tunicate and fully tunicate ears of corn. In the latter the glumes completely surround the grains.

GLUMELESS HYBRID SWEET CORN

And the Use of the *Vg* Gene in Producing Crossed Corn

WALTON C. GALINAT*

IN regard to sweet corn quality, it has been recognized for a long time that tenderness is equally as important as flavor. One of the important qualities of a good canning corn is freedom from adherent glumes which increase toughness and reduce total cut off by constricting the kernel base. Although several of the best canning varieties have been bred for short glumes, there are no commercial varieties, at present, with the distinctive advantage of being glumeless. Glumes may vary in length from several centimeters long in homozygous tunicate to nothing or a mere vestige as conditioned by the dominant gene, *Vestigial Glume*. Figure 1 shows a comparison of a naked flowered ear of vestigial glume sweet corn (*A*); a typical ear of sweet corn (*B*); an ear of half-tunicate (*C*); and a tunicate ear of corn (*D*).

In canned corn, a portion of the glume often adheres to the base of the whole grain and so increases toughness. In addition to this, loose glume material or chaff, along with corn borers and ear worms, must be washed out from the excised whole grains. In the production of cream-style corn, the corn borer may necessitate first cutting off the grains as in the production of whole grain corn and later, after washing, the whole grain is mascerated. The glume is equally objectionable in either case.

As for corn on the cob, the glume may be so long as to limit the edible part of the ear to the top or center of the grain. This forces most of the kernel contents out of the pericarp, with a considerable loss of the edible portion. This is the more serious because the embryo—rich in protein—is located in the base of the grain. In some cases the glumes are hard and sharp enough to cut the gums. Such glumes change the shape of the kernel to a shallow disk by constricting the kernel base.

Elimination of Glumes

The varied difficulties and complications brought about by the glume can be eliminated from hybrid sweet corn of the future by work of the sweet corn breeder and geneticist. There are now available glumeless strains of corn together with modifiers necessary for their use. The character, glumelessness, is conditioned by a dominant gene reported by Sprague[6] in 1939. Sprague realized the potential value of this glumeless character as a quality factor for sweet corn. He sent a sample of his *Vestigial Glume* field corn to Dr. W. R. Singleton at the Connecticut Agricultural Experiment Station in 1939. Since then it has been continuously backcrossed into P39 and more recently into other sweet corn seed parents at the Connecticut Station.

At first the glumeless character aroused little interest because of its effect on the tassels. Since the immature anthers were exposed to direct sunlight, the pollen was killed, making the plant mechanically male sterile. Hence it seemed to be impossible to get pollen from the naked tassels in order to self inbred lines for use in seed production. The glumeless lines could only be maintained by recurrent backcrossing. Several mechanical methods have been devised to simulate the glumed condition and so prevent dessication of immature anthers.[1]

The two mechanical methods which have met with most success in obtaining *Vg* pollen are; (1) the use of over-head tobacco shading cloth; and (2) the use of polyethylene cylinders to enclose the maturing tassels. The amount of good pollen obtained by these methods is usually small, although the immature pollen may be sifted out in the manner described by Mangelsdorf[3] for small pollen separation. Both of these methods are somewhat complicated and probably impractical for the commercial increasing of inbred seed.

Sprague[6] noted that some of the *Vestigial Glume* tassels had glumes approximately a third the normal length. He did not mention, however, the pollen shedding capabilities of these modified types. In the process of backcrossing the *Vg* gene into sweet corn seed parents, modified *Vg* types appeared with glumes ranging from a third to two-thirds normal length. These modified *Vg* tassels shed

*The Connecticut Agricultural Experiment Station, New Haven, Connecticut. Present address: Department of Agronomy, University of Wisconsin, Madison, Wisconsin.

pollen almost as abundantly as normal tassels. The glumes on a normal tassel are longer than those on its ear. This is also the case for the modified *Vg* plants, since the glumes on the ear are still reduced to a mere vestige, or, at most, are not long enough to form obnoxious chaff. These modified vestigial glume lines may be selfed and increased to indefinite amounts in the homozygous condition. It is preferred to have the *Vg* gene in the seed parents because of the improvement in seed shape and pollen production by the modified *Vg* tassels which may be limited under some weather conditions.

The *Vg* Gene in the Production of Crossed Corn

Since the unmodified glumeless lines are mechanically male sterile, they might be used in such a way as to eliminate the detasseling step in the making of hybrid corn seed. A type of mechanical sterility (indehiscent anther) has been used in hybrid tomato seed production by use of an electric vibrator to obtain pollen.[4] It appears simpler, in the case of *Vg* corn, to utilize the modifiers for the vestigial glume character rather than mechanical means to obtain pollen. A line cross or single cross could be used to cover up recessive modifiers and thus leave the crossing field seed parent mechanically male sterile. Detasseling of such fields would be unnecessary. Segregation for modifiers in the final hybrid could be used to provide enough pollen plants to insure a good seed set. Exact details relative to genetic control of pollen production for glumeless sweet corn hybrids are still in the process of being worked out.

The use of the genetic character male sterile-1 for the production of hybrid seed corn without detasseling was suggested by Singleton and Jones.[5] It required the difficult task of trying to separate the male sterile seeds from the fertile seeds by use of linkage to white and yellow seed colors. A similar system might be used to pick out the *Vg* seed from the normal segregants and so not require actual selfing but only backcrossing to normal to obtain 100 percent glumeless lots of seed for use in the crossing field. It would, however, also meet with the same difficulties of misclassification due to hetero-fertilization and crossing over.

Jones[2] has devised a system involving the use of a dominant fertility restorer in the pollen parent for cytoplasmically male sterile seed parent rows. If, in the long run, the use of cyto-male sterility proves impractical, although it appears quite promising now, the use of vestigial glume as a male sterile type should be considered. For the present, work on its quality value is emphasized.

In conclusion, by the proper application of genetic techniques, the use of the *Vg* gene in hybrid sweet corn now seems feasible.

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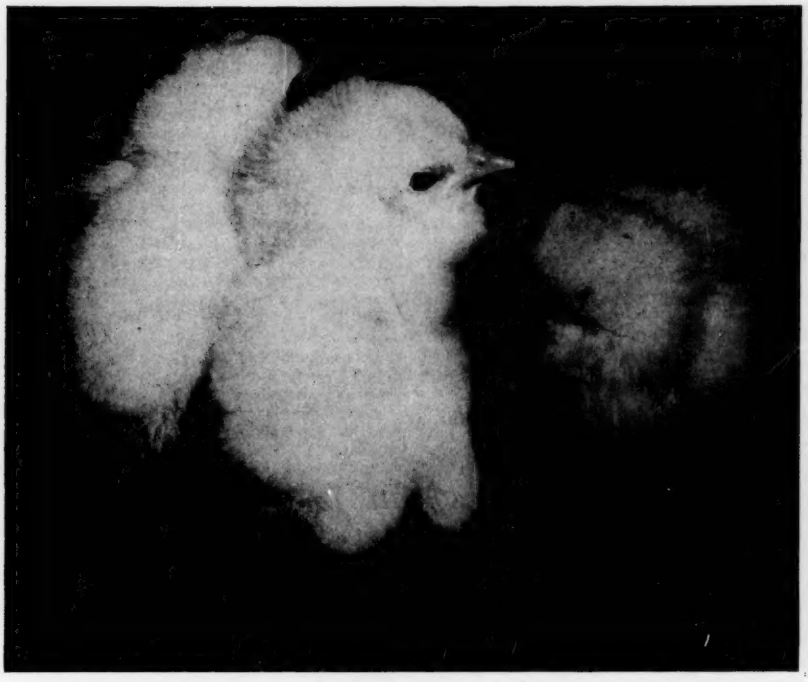
Dr. Li Reaches Pittsburgh

Dr. Thomas Parran, Dean of the Graduate School of Public Health, University of Pittsburgh, has announced the appointment of Dr. Ching Chun Li as a Research Fellow in Biostatistics to conduct studies on inheritance in relation to public health problems.

Dr. Li, who is an expert on population genetics, was graduated from the University of Nanking, China, 1936. He received the Doctor of Philosophy degree from Cornell University in 1940, and did further graduate work at the University of Chicago, Columbia University, and North Carolina State College. From 1946 to 1950 he was Professor and Head of the Department of Agronomy at the National Peking University of Peiping, China. He left this position when the Chinese Communist government forbade the teaching of the Mendelian principles of heredity because they are unacceptable to Communist ideology. Dr. Li's return to this country was made possible through the efforts of the Committee on Aid to Geneticists Abroad of the Genetics Society of America, under the chairmanship of Dr. Ralph E. Cleland, of Indiana University.

SNOW-WHITE DOWN IN THE CHICK*

F. B. Hutt†



MOST "WHITE" CHICKS ARE YELLOW

Figure 2

All three chicks are dominant white, but the two on the left are also snow-white. Their down contains no yellow pigment. Black flecks in the down of the two chicks to the right show that they are heterozygous for dominant white.

IN adult fowls, the dominant-white plumage of White Leghorns is indistinguishable in appearance from the recessive white of White Wyandottes, White Plymouth Rocks and some other breeds. Genetic differences among these breeds are somewhat more evident in the downy plumage of the newly hatched chicks. At that stage, some White Plymouth Rocks are bluish, or a smoky white, and others a light cream color. White Wyandottes are usually light cream and rather uniform in shade, but White Leghorns will vary all the way from pale cream to golden yellow. Chicks of these breeds (and of other white

*Number 25 in the author's series entitled "Genetics of the Fowl."

†Department of Poultry Husbandry, Cornell University Agricultural Experiment Station, Ithaca, New York.

ones) have one thing in common in that they are not pure white but always have a tinge of yellow in the down.

This note reports a different kind of white, — one that removes the yellow. Because this leaves the down as white as fresh snow, it seems appropriate to call it snow-white. To the best of the author's knowledge, this mutation has not previously been described.

Description

Unlike dominant, recessive, and albinotic whites, snow-white has no visible effect on melanic pigments, either in the down or in the definitive plumage. Its sole effect that has been recognized thus far is that it makes snow-white all down that would otherwise be cream, greenish white, or yellow. The mutation has no recognizable effect on later plumages, and as soon as the snow-white chicks lose their down they are indistinguishable from any other white ones. It does not remove red from the down.

Up to that point, the difference between snow-white and other white chicks is so great that there is never any doubt about the correct classification. It is true that among White Leghorn chicks some of the palest ones may appear to be white when compared with the others. That these differences in shade have a genetic basis was shown by Lamoreux and Hutt,[2] who differentiated by selection two strains, one characterized by dark yellow down, the other by a preponderance of chicks with pale down. However, the range in intensity of yellow normally encountered in White Leghorn chicks includes none that could be mistaken for snow-whites by anyone who has seen the latter.

The first bird found to carry snow-white was a pure Barred Plymouth Rock purchased in 1940. In subsequent years, many of his descendants were black, barred, and homozygous for snow-white. When these hatched, there was little or no difficulty in distinguishing snow-whites from the others by the shade of down shown in the head spot, on the tips of the wings, and on the ventral surface. These regions normally lack melanic pigment in barred chicks. In non-barred black chicks, which frequently have black down over the entire feathered surface, it is not so easy to recognize snow-white. The proportions of the two types that could not be classified as snow or not-snow among siblings hatched in two seasons were as follows:

	Chicks, Number	*Unclassifiable, Percent*
Black and barred	221	1.3
Black, not barred	27	29.6

In adult birds, whether barred or non-barred, dominant white or black, no trace of the snow-white mutation could be seen in the plumage, nor did it reduce the yellow pigmentation of the shanks, skin, and eye. Snow-whites lay eggs with yolks just as yellow as those of other hens.

Genetic Basis

All snow-white chicks are homozygous for an autosomal recessive gene, for which the symbol *sw* is proposed.

When the Barred Rock male, H 5143, which was the first bird known to carry *sw*, was mated with unrelated hens in 1941, no snow-white chicks were recorded among his 43 offspring. In 1942 he produced by unrelated females 31 chicks, all normal. Of his nine daughters that were mated to him, seven produced none with snow-white down, but some of these had only six or seven chicks, and hence might have carried the gene. The other two yielded 20 normal : 7 snow-white, a close fit to the ratio of 3 : 1 expected for a simple recessive character.

These few snow-white chicks of 1942 proved that the gene *sw* is autosomal, for, although two were lost to predators and hence could not be classified for sex, among the remaining five there were three males and two females. If this recessive mutation were sex-linked, all of these chicks would have been females, and their sire should have produced other snow-whites even by females unrelated to him.

This somewhat meagre evidence in 1942 that snow-white is a unifactorial, autosomal, recessive character was confirmed by the extensive data of later years, some of which are given in Table I. Because the mutation is manifested fully in both sexes, and because six columns are easier to follow than twelve, the data are not given separately for males and females. It will be noted that snow-whites mated *inter se* yielded only snow-whites, and that the back-crosses yielded approximately 1 : 1.

In addition to the various matings with snow-white males reported in Table I, five different heterozygous males were back-crossed (in various tests for linkage) to snow-white females. These yielded the following ratios:

	Progeny	
Male	*Not snow*	*Snow*
O 5003	118	104
Q 5005	104	87
Q 5006	114	136
Q 5007	57	68
Q 5008	25	46
	418	441

Among these chicks, as with the back-crosses shown in Table I, there was a slight excess of snow-whites. When results in the nine different matings are combined, the ratio is 727

not-snow : 767 snow, but the deviations from the expected 747 in each class are not statistically significant ($\chi^2 = 1.07$, P = *ca.* 0.3) and hence are attributable to chance. The slight excess of snow-whites shows that the mutants are just as viable as the others during the period of incubation.

Apart from all data considered thus far, there were 23 matings of snow-white females with unrelated males, and these yielded 178 chicks, none of which had snow-white down.

Tests for Linkage

Tests were made to see if *sw* showed any linkage with eight other genes that have already been assigned to autosomal linkage groups known for the fowl. All of these tests were made by back-crossing heterozygotes to multiple recessives, and the results can therefore be expressed simply as the ratio of parental combinations to new combinations in the resulting populations, (Table II).

Although these tests show no evidence that *sw* belongs in any of four linkage groups out of the five autosomal groups known (for details of these see Hutt[1] and Warren[3]), that possibility is not excluded. It is less likely with the *D M Po* group, since tests with both *D* and *Po* were negative, and these two genes are separated by a map distance of 61 cross-over units. However, the tests with *R* and *P* show merely that *sw* is not closely linked with either of these genes. It might subsequently prove to be linked with some gene remote from *R*, or from *P*, but in the same chromosome as either one. Tests with *P* seemed to show about 45 percent crossing over between that gene and *sw*, but the deviation (241:200) from a 1 :1 ratio is not significant in the 441 gametes tested.

A test for linkage of *sw* with *Mb* (muffs and beard) was also negative.

Discussion

At the present time, four genetically different kinds of pure white plumage may be found in adult fowls. These are dominant white (*I*), recessive white (*c*), autosomal albinism (*a*), and the depigmentation sometimes found in birds that were originally colored. A fifth type is the sex-linked imperfect albinism (*al*) which removes nearly all of the melanin but permits patterns, such as barring, to show faintly in the white feathers. The similarities and differences among these various kinds of white plumage, together with what is known of conditions causing them, have been recently reviewed elsewhere (Hutt[1]). They have one thing in common, *i.e.*, they result from processes that interfere with the production of melanin, or with the survival of melanophores. These same processes apparently have no effect whatever on the carotinoid pigments responsible for the yellow color in the skin and shanks, and in the egg. This is not surprising because these pigments, unlike the melanins, are not produced in the cells of the body, but come from the feed.

Snow-white is a mutation with an effect entirely different from that of the other kinds of white listed above. It does not affect the melanins, but prevents formation of the pigment responsible for the yellowish tinge of the down feathers. So far as the writer is aware, the chemical nature of that pigment is unknown. It was found by Lamoreux and Hutt[2] to be insoluble in petroleum ether, and in chloroform, and hence is not likely to be xanthophyll, which is responsible for almost all of the color in egg yolk. It is partially soluble in a mixture of sulphuric acid and acetone, and not likely to be riboflavin. While birds homozygous for *sw* apparently differ from others in some intra-cellular chemical process, that difference seems to have no adverse consequences, for snow-white chicks were no less viable than their normal siblings either after hatching or before.

TABLE I. Ratios in progeny of snow-white males mated with females of three genotypes. Phenotypes of progeny are "not snow" = +; "snow" = —.

Year	♂ *sw sw*	♀♀ *Sw Sw* +	♀♀ *Sw Sw* —	♀♀ *Sw sw* +	♀♀ *Sw sw* —	♀♀ *sw sw* +	♀♀ *sw sw* —
1943	K 6001	43	0	8	8	0	4
"	K 6011	109	0	39	39	0	10
1944	M 152	..	..	111	136	0	91
1945	O 5004	..	..	151	143	..	..
1946	O 5005	42	0	..	..	..	..
"	O 5006	..	..	..	..	0	68
1950	Q 5015	16	0	..	..	0	145
	Totals	210	0	309	326	0	318

TABLE II. Results in back-crosses made to test for linkage of *sw*.

Linkage group	Genes tested		Parental combinations	New combinations
Cr I F	Crest	*Cr*	117	136
	Dominant white	*I*	151	143
	Frizzling	*F*	118	127
D M Po	Duplex	*D*	100	90
	Multiple spurs	*M*	33	46
	Polydactyly	*Po*	115	106
R Cp U	Rose comb	*R*	105	91
O P Ma	Pea comb	*P*	241	200
Independent	Muffs and beard	*Mb*	71	71

The mutation is a good one for studies of linkage because it can be recognized at hatching and even in chicks that die during the last few days of incubation. When tests were made for linkage of snow-white with rose comb and pea comb, the 637 chicks hatched were used to make a laboratory exercise in linkage for a class in genetics. Since the rose, pea, and single combs are not difficult to distinguish, and snow-white is recognizable at a glance, these chicks, new lots of which were classified in three successive weeks, proved ideal for demonstrating the independent segregation of the three pairs of alleles concerned. For some classes there is a special advantage in supplementing the usual laboratory material with a species that is (1) an animal, (2) a vertebrate, and (3) a domestic animal. The prospective specialist in bovine obstetrics is not always happy when counting kernels of corn or squinting through a lens in search of forked bristles on a fruit fly.

Summary

Snow-white (*sw*) is a unifactorial, autosomal, recessive mutation, which, in the homozygous state, removes the color from the down of chicks that would otherwise be creamy, yellow, or greenish white in color. The contrast between snow-whites and other whites is so great that accurate classification can be made at a single glance. It has no recognizable effects in later plumages, or on black pigment, and does not interfere with the deposition of carotinoid pigments in the shanks, skin and eggs. Red down is unaffected.

Viability of snow-white chicks and embryos is unaffected by the mutation.

In tests for linkage it proved to be independent of nine different genes, eight of which are "markers" for four of the five autosomal linkage groups known in the fowl.

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An Hereditary Inability to Tolerate Polysaccharides?

SOME evidence supports the view that there is a familial tendency toward celiac disease [chronic diarrhea in childhood accompanied by malnutrition], as Haas found it in several generations of the same family, in twins, in brothers and sisters, in cousins and more distant relatives. But more than one case is found infrequently in the same family at the same time. Lehndorff and Mautner noted that although nothing conclusive could be shown from family histories, it was astonishing, in view of the rarity of the disease, how frequently it struck close relatives—twins, siblings, cousins.

* * *

The familial background of the patient is important, since it is not at all unusual to find the disease in siblings and cousins. As a matter of fact, we have treated four children of a physician, all of whom had celiac disease and another family with 5 cases. The economic level of the family seems to have little to do with the disease, nor do national or racial origins. With the exception of colic or vomiting in the neo-natal period, which appears in the histories of a significant proportion of cases, no other prior disease states seems to have any connection with celiac disease.

* * *

The *Symptoms* of celiac disease will persist so long as polysaccharides (complex carbohydrates) are ingested and will disappear only if monosaccharides (simple carbohydrates) are used with the addition of protein and fats, the latter being well utilized if the polysaccharides are excluded from the diet. These observations are based on a clinical experience of 30 years and have been substantiated by laboratory investigation as well.—Sidney V. Haas and Merrill P. Haas. Management of Celiac Disease. J. B. Lippincott Company. Philadelphia, 1951.

MORE ABOUT LEPESHINSKAYA'S HOME-BREWED CELLS

IN the preceding issue of this JOURNAL, mention was made of the "discovery" by Professor Olga Lepeshinskaya of the origin of cells by spontaneous generation. Biologists in this country will be interested in further details regarding this truly incredible development. It is our pleasure, therefore, to present herewith translations of two articles from Berlin newspapers. The first of these is from the *Tägliche Rundschau,* (East Berlin, July 12, 1950). The second is from the *Tagesspiegel.* (West Berlin, June 20, 1950). These articles are presented in reversed sequence because Professor Nachtsheim's commentary is the perfect answer to Dr. Khrushchov's dissertation on the development of cells out of non-cellular matter.

NEW DEVELOPMENTS IN CELL THEORY*

A Significant Discovery of the Soviet Biologist O. B. Lepeshinskaya

DR. G. KHRUSHCHOV

SOVIET biology, which leads onwards in the progressive materialistic direction, is making a courageous break with the old traditions, standards and conceptions that hinder the development of the science of life, and is creating new, progressive views whereby the Soviet people are given opportunity for effectively transforming nature in the interests of the people. An example of such creative scientific work is furnished by the researches of the Soviet biologist Prof. Olga Lepeshinskaya on extremely important problems of cell theory.

The Theory of Schwann and Schleiden and Their Distorters

The theory of the cell, created in the first half of the 19th century, represents an outstanding theoretical achievement of biology, by which the unity of the organic world has been proved and, with this, the basis of the theory of the development of living nature—the evolution of animals and plants—has been created. Friedrich Engels pointed out that the cell theory developed by Schwann and Schleiden was, along with the discovery of the law of transformation of energy and the founding by Darwin of the theory of evolution, the great achievement of science by means of which the predominance of metaphysical and idealistic views concerning nature was brought to an end and the way cleared for the dialectical Marxist explanation of the phenomena of nature.

The founders of the cell theory rightly held the view that the problem of the origin and development of cells is an integral part of these theories. Schleiden and Schwann also made the first attempt to solve this problem: this was the theory, put forward by them for purposes of discussion, concerning the origination of the cells in animal and plant organisms from a living, microscopically structureless mass.

The cell theory, the greatest achievement of 19th century biology, to which the idea of development is basic, was inconvenient for the scientific reactionaries, and was distorted and tailored to fit their idealistic and metaphysical views.

Like the "neo-Darwinian" followers of Weismann in their relation to Darwin's theory, so too the "cellularists" have since the middle of the past century recognized in words the theory of Schleiden and Schwann, but have in fact done everything to dilute it and to eliminate its materialistic basis, the idea of development. Especially active in this direction was the German pathologist Rudolf Virchow, the originator of so-called "cellular pathology," one of the most reactionary biologists and medical men of the 19th century, a professed anti-Darwinist who was most sharply criticized by Friedrich Engels.

In Virchow's hands the cell theory became transformed from a theory based on the idea of development into a rigid collection of metaphysical dogmas and idealistic representations of biological procesess. In this distorted form, as one of the most essential bases of the reactionary doctrines of Weismann and Morgan, Virchow's cell theory became the dominant trend in biology and medicine and for a long time held up the progressive development of the science of life.

*Translated from *"Tägliche Rundschau"* (East Berlin), of July 12, 1950.

It is the achievement of O. B. Lepeshinskaya that she has relentlessly and thoroughly exposed the reactionary nature of all doctrines of cell theory that followed in Virchow's direction. In accordance with the guidance of Stalin concerning the necessity of criticizing antiquated scientific theories, and by applying to biological phenomena, in consequence, Lenin's and Stalin's theory of development, she disproves in her works, with the aid of extensive material, the doctrines of Virchow which for a long time have been considered to be unalterable truths. *These investigations signify a new stage in the etsablishment of a really materialistic cell theory,* which opens up grand perspectives for the mastery of the definitive laws of the organic world.

The cell develops out of non-cellular matter also. All basic dogmas of Virchow ("Every cell arises only from a cell," "There is no life outside of the cell," "Life begins only with the cell," "The organism is a sum of cells") which deny the principle of development are being subjected to a devastating criticism in the works of Olga Lepeshinskaya. The accumulation of facts derived from her own researches, on which this truly fundamental critique is based, shows with great clarity that *Virchow's dogmas do not correspond to reality,* that they were falsely attributed to nature.

Through the observations of numerous investigators on the development of the egg cells of birds and fish, which are rich in yolk, the occurrence of so-called "yolk globules" beneath the developing embryo was established a long time ago. Some of these globules are nothing but an accumllation of yolk granules held together by the egg plasma; others contain nuclei and are indisputably cells. In the era before the investigations by Olga Lepeshinskaya most cytologists and embryologists, following the generally recognized theory that a cell can originate only from a cell, regarded the non-nuclear "yolk globules" as non-living masses of nutritive material: the nucleated ones, however, as either cells which had been eliminated from the embryo (in birds) or as transformed spermatozoa which had entered the egg cell in large numbers at fertilization (in fish). Olga Lepeshinskaya has shown by painstaking investigations that *the nucleated "globules" develop from non-nucleated ones, and in fact by means of the gradual origination within them of the structural elements, above all the nucleus, which are characteristic of a cell.* It was also possible, by means of special experiments, to demonstrate the occurrence of the same processes of development of cells from yolk globules outside of the organism, and to obtain documentary confirmation of these events by means of moving pictures taken with the aid of a microscope.

This was the irrefutable proof that the formation of new cells in the organism does not take place only by cell multiplication but also by their direct development out of non-cellular living material. Therefore not only are the organism's cells capable of development but also the living material which is not organized into cells.

Olga Lepeshinskaya was later able to confirm this discovery through numerous investigations of her own and through those of her students and co-workers. Thus it has been demonstrated that when living matter is prepared from hydra, a very simply organized fresh-water animal, by grinding it up and then freeing it of residual cells and cell-parts with the aid of filtration, out of this material cells of the animal again develop, and go through the initial stages of development of a whole organism.

Numerous observations by Olga Lepeshinskaya have further shown that in a developing hen's egg the very first blood cells in the so-called "blood islands" also consist of non-cellular yolk globules. Finally Olga Lepeshinskaya has found, through investigations of the healing of wounds in adult animals, that the cells and the inter-cellular structural elements which rebuild the tissue arise from the non-cellular material which fills the wound while it is bleeding. These observations have not only confirmed Olga Lepeshinskaya's most important theses but have shown that in the adult animal organism also there is living matter which can develop into cells.

BIOLOGICAL PHANTASIES*

New Developments in the Case of Lysenko

PROFESSOR HANS NACHTSHEIM

ACCORDING to a communication from the TASS news agency investigations of the biologist Olga Lepeshinskaya in the field of the formation of new cells in living organisms have brought forward new proofs of the correctness of the theories of Lysenko and Michurin. The above biologist is said to have succeeded in showing that the formation of

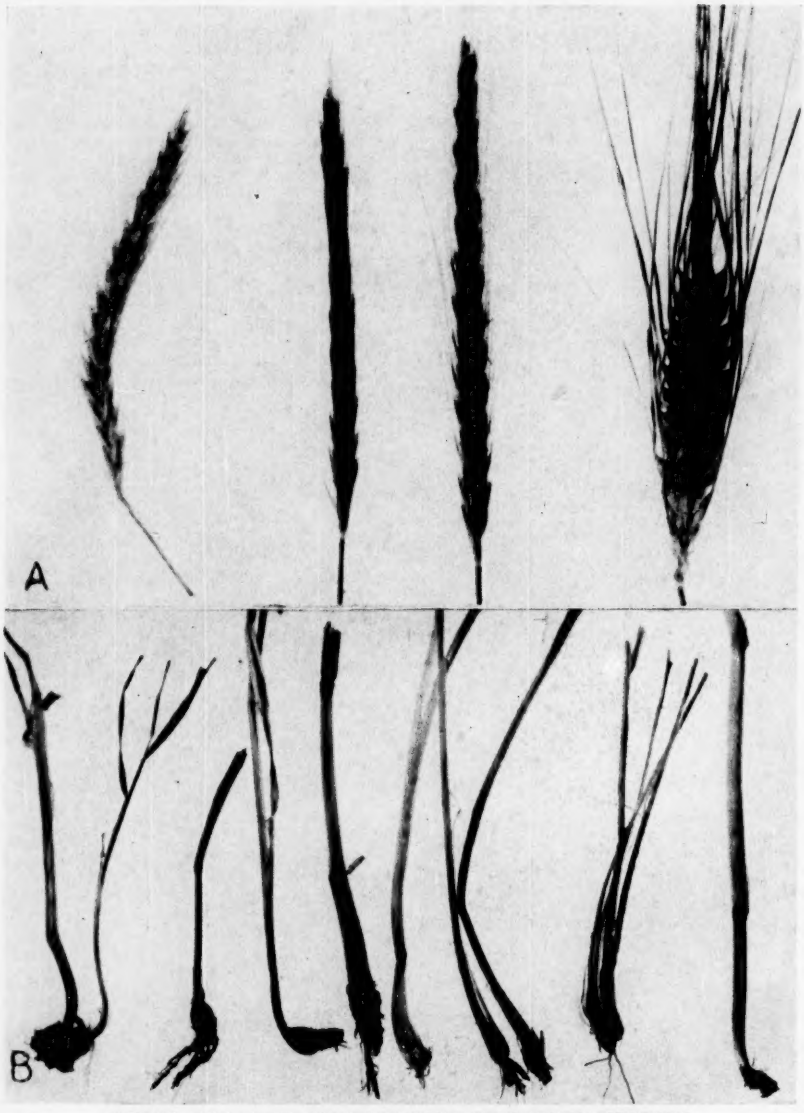
*Translated from *"Tagesspiegel"* (West Berlin), of June 20, 1950.

new cells in living organisms can take place not only through the multiplication of the cells themselves but also through direct development from so-called structureless material. At a conference of the Soviet Academy of Sciences this scientist is reported to have demonstrated the possibility of living cells developing from the structureless albumen of the eggs of various birds. The albumen is said to be not merely a lifeless nutritive element, but living material which is capable of developing and forming cells. The investigations represent, according to TASS, a new milestone in the materialistic theory of the nature of cells and open a new outlook for demonstrating the basic principles of the organic world. Trofim Lysenko called the researches of Olga Lepeshinskaya an "important contribution" for the development of his theory.

So much for the TASS communication. What lies behind it? Nothing new. Nearly twenty years ago Olga Lepeshinskaya had in a series of publications sponsored the view that the origination of cells in the multicellular organism takes place not only through division but also through their formation from protoplasmic masses, by "transformation of the living substance." She believes she has observed the origination of cells, blood islands and tissues from detached yolk globules of the hen's egg. Even chromosomes and division figures are supposed to arise *de novo* in this way. Olga Lepeshinskaya thereby returns to a view which the founders of the cell theory, Matthias Schleiden and Theodor Schwann, sponsored in the '30s of the past century: namely, that cells arise from an organic mother plasma, through its free formation of cells. It is the achievement of Rudolf Virchow to have demonstrated that there is no "free formatiton of cells." Since 1855 the expression voiced by Virchow, "Omnis cellula e cellula," has held: that every cell arises from a call. The contrary claims of Lepeshinskaya were not taken seriously either in her homeland or in other countries. N. K. Koltzoff, one of the most significant figures of this century among Russian biologists, stated already in 1934, regarding the investigations of Lepeshinskaya, that the free origination of nuclei with a complete garniture of chromosomes was just as fantastic as if she were to claim that she had produced a living chicken by spontaneous generation.

It is highly surprising that the two spinners of phantasies, Lepeshinskaya and Lysenko, have only now discovered one another. Obviously each one now seeks to clamber up on the other one. Lysenko, too, is more and more losing the ground of actuality from under his feet. In his most recent publication ("J. V. Stalin and the Michurinist Agrobiology," in the journal *"Selection and Seed Culture,"* 1950, Volume 1) he asserts no more and no less than that he has succeeded in changing wheat into rye. Yes—wheat into rye! I shall quote him literally: "On the basis of this investigation a series of scientists and agronomists has in the year 1949 shown quite convincingly that in the regions of foothills and mountains under unfavorable conditions of wintering over, and especially in plots having conditions unfavorable for development, winter wheat can change over into rye. Assertions of practical men have long been known to the effect that such metamorphoses, such a change-over of wheat into rye, is possible. Science, however, when proceeding only from the standpoint of a theory of "smooth evolutionism," has looked with *a priori* disfavor upon the possibility of the transformation of cells of one botanical species into another." A well known biologist with whom I spoke about the matter commented pertinently that Lysenko might just as well have asserted that a woman who lived in the primeval forest could bring a chimpanzee child into the-world.

To us biologists it can only appear as right that Michurinist biology in Soviet Russia is undergoing this development. Even the few biologists who, because of their political attitude, still believe they have to defend Lysenko, such as the German zoologist W. Ludwig, who not long ago gave lectures on genetics by invitation at my former chair in Humboldt University, will perhaps allow themselves to be convinced anyway, at this development, that the "case of Lysenko" does not belong on the rostrum of the biologist, but rather in the hands of the psychiatrist.



SPIKES AND ROOT DEVELOPMENT OF BARLEY HYBRIDS

Figure 4

A—(left to right) a spike of wild perennial barley (*H. bulbosum*), two spikes of the F_1 hybrid, and a spike of the Moore variety of cultivated barley (*H. sativum*). *B*—Root development of the same series, the root on the extreme left being wild barley, and that on the extreme right, the Moore variety. The seven roots in the middle show the variation in bulb development in the F_1 plants. Magnification: *A* ¼ and *B* ½ natural size.

EMBRYO CULTURE OF BARLEY SPECIES HYBRIDS

Cytological Studies of *Hordeum sativum* × *Hordeum bulbosum**

C. F. KONZAK, L. F. RANDOLPH AND N. F. JENSEN†

HYBRIDIZATION of common barley, *Hordeum sativum*,‡ with its wild perennial relative, *Hordeum bulbosum*, was accomplished first by Kuckuck[3] in Germany. A single F_1 plant was obtained from 4578 pollinations but attempts to backcross it to each of its parents were unsuccessful. The hybrid nature of this plant was established by chromosome counts from root-tip tissue, but no other cytological studies were reported. Similar experiments were performed later by Smith[6] in the United States and by Vinogradova[9] in Russia. Various strains of cultivated barley were used in these experiments but no viable hybrids were obtained. Vinogradova obtained a seedling from this cross with *Hordeum bulbosum* as the seed parent, but the seedling died in an early developmental stage and no chromosome count was made.

Most varieties of winter barley are deficient in winter hardiness and many are also susceptible to mildew and other diseases. *Hordeum bulbosum* apparently possesses a fair degree of winter hardiness.[4] Its resistance to powdery mildew (*Erysiphe graminis* f. *hordei*) at Ithaca, N. Y., is indicated by the fact that it has remained free from this disease when common barley grown nearby in the greenhouse and out-of-doors, has been almost completely covered by the fungus. Whether it also possesses genes which control resistance to other diseases has not been determined.

In undertaking to cross *H. bulbosum* with various cultivated varieties of *H. sativum* it has been demonstrated in the course of the present study that hybrids can be obtained by recourse to the embryo culture technique. Furthermore, cytological observations of meiotic chromosome behavior in the hybrid have indicated that sufficient compatibility may exist between chromosomes of these species to make possible a transfer of desired characters from one species to the other.

The Parental Plants

The parents of the cross consisted of single plants of each of four spring barley varieties, Stephan C. I. 8051, Freja C. I. 7130, Moore C. I. 7251, and Bolivia C. I. 1257, the winter barley variety Wong C. I. 6728, and a self-fertile plant of *Hordeum bulbosum* (Figure 3*A*).

Cultivated varieties of barley are self-pollinated annuals and have leaves that are typically non-hairy. *H. bulbosum*, according to Kuckuck[3] and Lein,[4] is a self-sterile, naturally cross-pollinated perennial species which has leaves that are sparsely pubescent. However, some of the plants of this species which were grown for this study were rather highly self-fertile. The seed from which these plants were grown were obtained through Dr. G. A. Wiebe, U.S.D.A., Beltsville, Maryland.

Development and Culture of the Hybrid Seed

When *H. sativum* was used as the pistillate parent and *H. bulbosum* as the pollen parent, partly developed seeds were produced by 18.4 to 97 percent of the ovules, depending on the variety of cultivated barley used in making the cross. In the experiments of Kuckuck, the seed set was 9.8 percent (Table I). In certain crosses, seeds started to form in most of the ovules in exactly the same manner as in crosses between varieties of common barley. The reciprocal cross was attempted and found

*Paper No. 269, Department of Plant Breeding, Cornell University, Ithaca, New York.

†Graduate Assistant, Department of Plant Breeding, Professor of Botany and Professor of Plant Breeding, respectively, Cornell University, Ithaca, New York. The authors wish to acknowledge their indebtedness to Drs. A. M. Srb and H. H. Smith of the Department of Plant Breeding, Cornell University, for their valuable advice during the course of this study and in the preparation of this manuscript.

‡The species designation *Hordeum sativum* Jess. is here used collectively to include both 2-rowed and 6-rowed types, common examples of which were used in this study.

to be incompatible, in complete accordance with Kuckuck's results.

Growth of the hybrid seeds in the early stage was somewhat slower than that of hybrid seeds involving varieties of cultivated barley that were pollinated at the same time. Development of the hybrid seed continued for varying periods of time, but in no case beyond the 15th day after pollination. Thereafter, there was complete cessation of growth. If these defective seeds had been permitted to remain on the plant until the normal date of maturity, it seems highly improbable that any of them would have germinated.

The embryos were excised and transferred to the sterile culture medium recommended by Randolph and Cox[5] when the hybrid seeds reached their maximum development on the plant and before degeneration commenced. This critical stage of development was identified by its association with a change in the color of the seeds.

Before the embryos were excised, the freshly harvested immature seeds were treated for one to three minutes with a solution composed of nine parts of water and one part of chlorox. The treated seeds were then rinsed in sterile water and the embryos were removed with flattened dissecting needles which had been previously sterilized and immersed in a solution of hexylresorcinol (ST-37) diluted with an equal part of water. This solution has desirable germicidal properties and contact with the embryos for brief periods of time causes no detectable injury. Transfers were made in a covered inoculation chamber which had been sprayed with a one percent solution of phenol. In handling the seeds as the embryos were being removed the fingers were frequently dipped in 50 percent ethanol, shaken, then dipped in the ST-37 solution.

The excised embryos were placed on the surface of the culture medium in one-ounce glass vials and incubated at 28°C for several days. When an appreciable amount of additional growth was apparent, they were transferred to a chamber which was lighted continuously with fluorescent lamps and kept at a temperature of approximately 23° to 27°C. Contamination with microorganisms occurred in only a very limited number of culture bottles.

Only 11 embryos of the 183 excised produced normal seedlings in culture. These 11 seedlings were subsequently transferred to soil in pots, where they continued to grow normally. Other embryos produced either a normal-appearing root and no shoot, or a shoot and no root in the culture bottles. Repeated transfer of such defective seedlings to a fresh culture medium failed to induce them to develop normally. Most of the remaining embryos made a limited amount of growth, but the growth was often restricted to the formation of a mass of undifferentiated tissue.

TABLE I. Comparison of Crossability

	Pollinated Flowers	Seed Set		Embryos Excised	Hybrid Seedlings Obtained
		No.	%		
Kuckuck's Results:					
H. sativum × *H. bulbosum*	4578	449	9.8		1
Reciprocal	1200	0	0		0
Results of the Present Study:					
H. sativum variety Stephan × *H. bulbosum*	65	12	18.4	12	0
H. sativum variety Freja × *H. bulbosum*	80	16	20.0	16	0
H. sativum variety Moore × *H. bulbosum*	358	133	37.1	121	6
H. sativum variety Wong × *H. bulbosum*	117	65	55.5	10	2
H. sativum variety Bolivia × *H. bulbosum*	43	41	97.6	24	3
Reciprocal	121	0	0	0	0

Characteristics of the Hybrids

In general, the hybrids were not intermediate between the parental forms. During their early growth a compact rosette resembling that of the wild species was formed. However, hybrids having the spring barley parentage flowered earlier than those having winter barley parentage. The spikes of all plants resembled those of the male parent very closely. Typical spikes of a hybrid and its parents are shown in Figure 4*A*. The anthors in the florets of the F_1 plant were observed to be about intermediate in length between those of the two parents. Most of the pollen was severely shrunken and a wide range of pollen size was apparent, as shown in Figure 5*K*, *L*, *M*. The leaves of the various hybrid plants differed in width, and in the intensity of green coloration; some plants were non-hairy, others were sparsely pubescent like the *H. bulbosum* parent, and one was highly pubescent. All of the hybrids were quite vigorous, some more so than others. Variation also occurred in the bulbous character. Two of the F_1 plants formed a bulb of almost the same size and shape as that produced by *H. bulbosum*. In others the bulb was smaller, or smaller and elongate, and in one plant there was no swelling, though the stem between the basal nodes was solid (Figure 4*B*). All plants appeared to have inherited at least part of the perennial nature of the wild species. A plant of *H. bulbosum* is shown in Figure 3*A*, and one of the hybrids in Figure 4*B*.

TABLE II. Average Number of Cells with Multivalents.

Female parent	Plant	Percent cells with multivalents		
Moore	17-1	66.96	56.56	67.45
	17-5	62.50		
	17-10	50.72		
	24-3	67.61		
	24-8	51.26		
Bolivia	32-7	84.15	83.44	
	32-9	84.07		
Wong	26-6	81.75		

Since the F_1 progenies involved sister seedlings from crosses in which the seed parents were uniform varieties of common barley, it is probable that the variation noted was due to a varying genotypic constitution of the *H. bulbosum* parent. In this connection it should be noted that *H. bulbosum* is a tetraploid and the hybrid seedlings were triploid.

Cytological Behavior of the Hybrids and their Parents

Bulbous barley (*H. bulbosum*), has been shown by Berg[1] to be an autotetraploid with a somatic chromosome number of 28 and to have frequent quadrivalent association of the chromosomes. A diploid ($2n = 14$) form of this species was reported recently by Lein,[4] but an attempt to obtain material of the diploid for these studies was unsuccessful. The tetraploid plant used in the present study was observed at the first meiotic metaphase to form varying numbers of quadrivalents and bivalents, and occasionally one or two trivalents together with an equal number of univalents. Figure 5, *B* and *C*, show typical metaphase I groups of *H. bulbosum* chromosomes. The configurations indicate that both alternate and adjacent types of chromosome disjunction occur. Homology between its genomes thus appears to be almost complete.

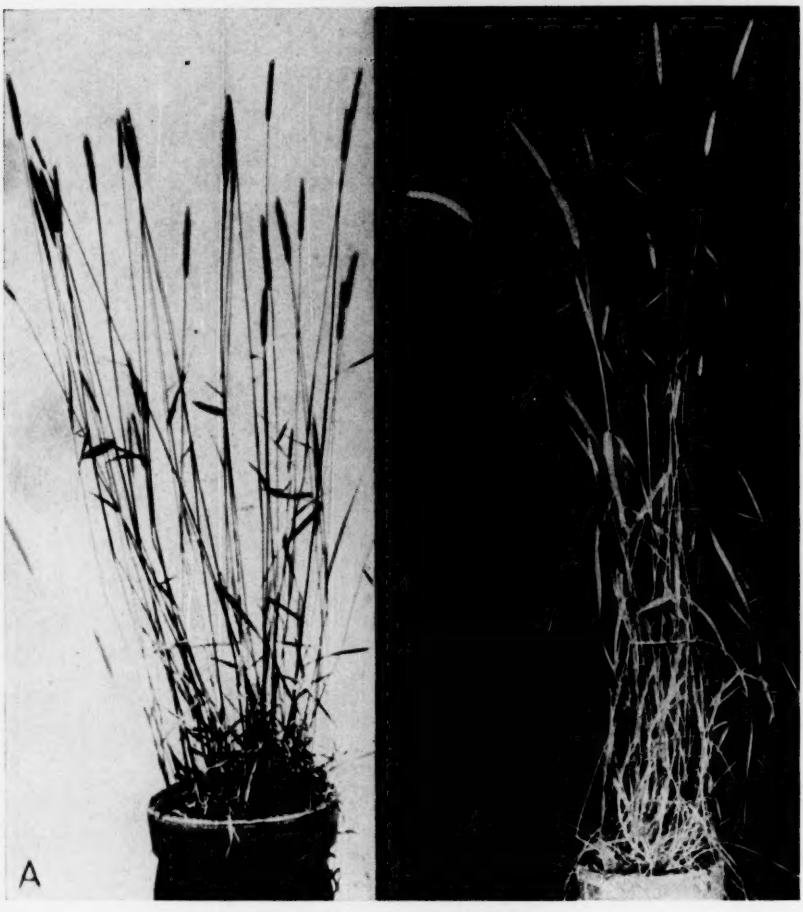
Cultivated barleys are all diploids with a somatic chromosome number of 14.[2] Meiosis was found to be normal in the seed parents of the hybrids obtained in these studies; Figure 5*A* shows the usual metaphase I associations that were observed.

The F_1 hybrids were triploids, as expected, with 21 chromosomes in their somatic cells. This count was first determined from root-tip

TABLE III. Chromosome Associations Observed at Metapsase I in Sporocytes of *Hordeum sativum* × *Hordeum bulbosum* Hybrids

Plant Number	$6_{II}9_I$	$7_{II}7_I$	$8_{II}5_I$	$9_{II}3_I$	$1_{III}5_{II}8_I$	$1_{III}6_{II}6_I$	$1_{III}7_{II}4_I$	$2_{III}4_{II}7_I$	$2_{III}5_{II}5_I$	$2_{III}6_{II}3_I$	$3_{III}3_{II}6_I$
17-1	1	41	4		1	46	1		12	2	
17-5		8	1			8			2		
17-10	2	125	9	1	5	86	5		29		
24-3		51	5	1		63	8		26	7	
24-8	3	52	3		2	34	3		11	1	
32-7		19	7	3		47	10		40	16	
32-9	2	19	4		3	43	6	1	35	2	1
26-6		19	6		6	38	9	2	29	6	1
Total	8	334	39	5	17	365	42	3	184	34	2

Plant Number	$3_{III}4_{II}4_I$	$3_{III}5_{II}2_I$	$4_{III}2_{II}5_I$	$4_{III}3_{II}3_I$	$5_{III}2_{II}2_I$	$1_{IV}6_{II}5_I$	$1_{VI}1_{III}5_{II}4_I$	$1_{VI}2_{III}4_{II}3_I$	Total Cells Scored
17-1	4								112
17-5						2	2	1	24
17-10	9			3			4		278
24-3	9	3			2		1		176
24-8	3					5	2		119
32-7	21	7		3	2	1	5	2	183
32-9	16	4	1	13	3		3	1	157
26-6	6	1			1	3	4	6	137
Total	68	15	1	19	8	11	21	10	1186



EMBRYO CULTURED HYBRID

Figure 3

A—is a plant of wild perennial barley; *B*—is a hybrid between this species and the Moore variety of cultivated barley produced by embryo culture. By excising the embryos and raising them on a nutrient medium eleven hybrid plants were brought to maturity. No viable mature seeds were obtained.

sections and later from aceto-carmine and aceto-orcein smears of microsporocytes. Observations were made of meiotic stages in eight of the 11 hybrid plants.

During prophase I of microsporogenesis both single and double strands were observed. In the pachytene preparations that have been studied the chromosomes were characteristically tangled and it was impossible to trace them accurately. However, in certain cells synapsed and unsynapsed parts of chromosomes could be distinguished, and occasionally an inversion loop was noted.

At metaphase I, varying numbers of univalents, bivalents and trivalents were observed and not infrequently a quadrivalent was present, as shown in Table III.

The average number of cells with multivalents in the F_1 plants is shown in Table II as a percentage of the number of cells scored. Where Moore was a parent the weighted average was 56.56 percent, while in the F_1 plants having Bolivia and Wong as female parents this figure was 83.44 percent. The weighted average of cells with multivalents for all parents was 67.45 percent.

The fact that the hybrids from the variety Moore exhibited an appreciably lower frequency of multivalents than those from the varieties Bolivia and Wong suggests that Moore differs from these two with respect to genes affecting chromosome homology as expressed in their synaptic behavior in the sporocytes of the hybrid plant and affecting crossability with *H. bulbosum*. The significance of these observed differences in chromosome behavior will be discussed later in relation to the general problem of cross incompatibility.

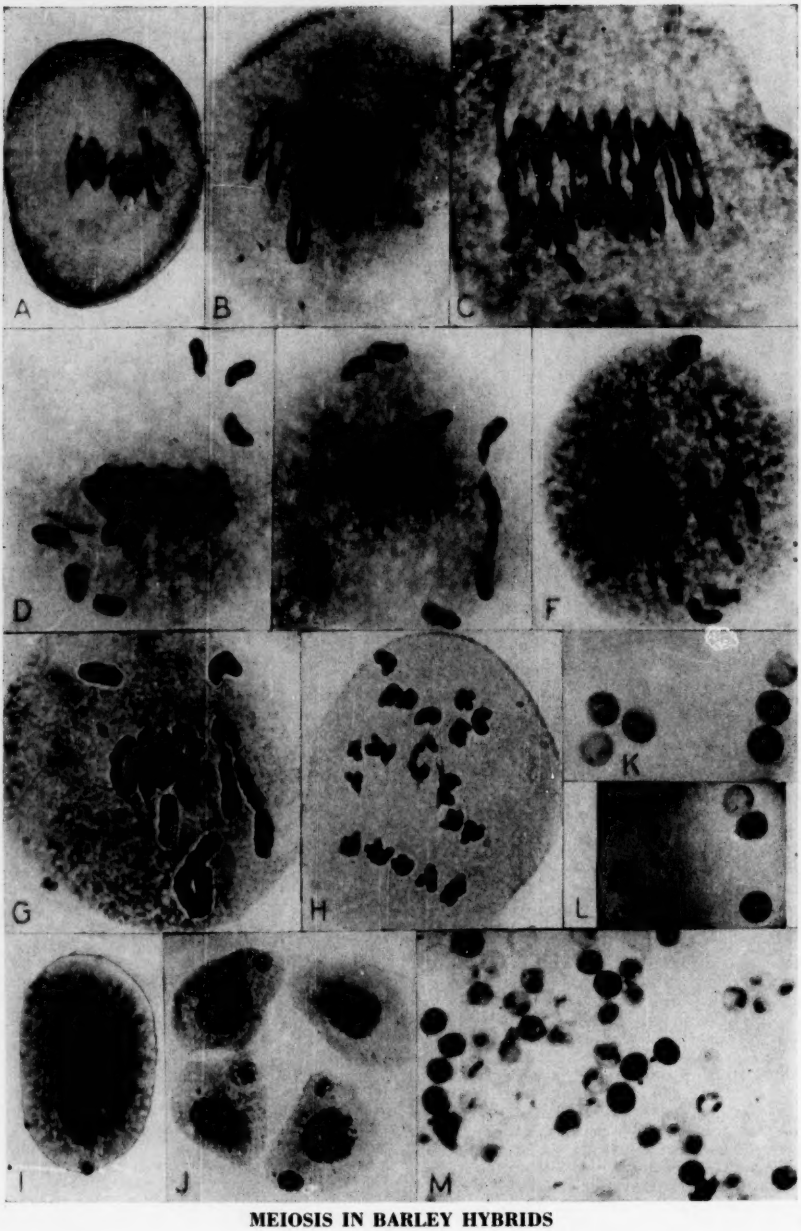
The number of trivalents present in metaphase I of the hybrids varied from 0 to 5. The observed number of bivalents and univalents was influenced not only by the frequency of trivalents but, in addition, desynapsis of bivalents in the late prophase not infrequently increased the prevalence of univalents. More than the expected number of bivalents, or varying numbers of bivalents and multivalents in excess of the expected number of seven, were noted with a frequency that could not be attributed merely to occasional nonhomologous association. For example, among the 1186 cells that were observed, there were five with nine bivalents and three univalents; 39 with eight bivalents and five univalents; 42 with one trivalent, seven bivalents, and four univalents; 34 with two trivalents, six bivalents, and three univalents; and five with three trivalents, five bivalents, and two univalents.

Atypical bivalents were frequently noted in the cells with more than the expected number of synaptic associations. Some of these were heteromorphic, one member of the pair being noticeably longer or otherwise morphologically different from the other. These atypical bivalents showed a tendency not to be regularly arranged on the metaphase plate and resembled what might be expected if homology were limited to restricted regions of the chromosomes (Figure 6*A*). Since it was often very difficult or impossible to distinguish these unusual bivalents from normal bivalents the two categories were classed together in summarizing the data in Table III. Their inclusion as normal bivalents increased the total number of synaptic associations. In connection with the suggested interpretation of these atypical bivalents it is noteworthy that Tometorp[8] observed a single bivalent in 5.6 percent of the microsporocytes of haploid cultivated barley. Other examples of limited chromosome pairing, possibly due to duplication of segments, are cited by Stebbins.[7]

A condition best described as an extreme stickiness of the chromosomes that was obviously not a fixation artifact was noted occasionally in the hybrids (Figure 6*B*). In about five percent of the sporocytes there were also examples of chromosome adherence which seemed to be caused by an unusual amount of centromere stickiness. These associations involved end connections of individual chromosomes or pairs of chromosomes with what appeared to be the centromeres of other chromosomes (Figures 6*C-F*). It should be emphasized, however, that the above-mentioned anomalous associations at diakinesis and metaphase I occurred in only a relatively small proportion of the sporocytes examined, while the majority of chromosome associations were as expected in typical triploids.

At metaphase I the bivalents, trivalents, and quadrivalents were oriented on the equatorial plate, the univalents ordinarily were scattered throughout the nucleus and rarely reached the metaphase plate until later. The trivalents disjoined two from one in the usual manner at anaphase, and disjunction of the quadrivalents was either two from two or three from one (Figure 5*E-G*). The univalent chromosomes behaved irregularly at anaphase I. Those that reached the plate following the disjunction of other chromosomes usually split longitudinally and the daughter chromatids then moved poleward. Other univalents apparently never reached the plate and remained undivided at or near the telophase groups as daughter nuclei were formed. Chromosomes not included in the daughter nuclei formed micronuclei. The behavior of univalents in division I is illustrated in Figure 5*D-H*. Lagging chromosomes, presumably derived from univalents that had divided in the preceding anaphase, were present in many of the second anaphases. An example of this is shown in Figure 5*I*. At the spore quartet stage, micronuclei were present in most spores (Figure 5*J*).

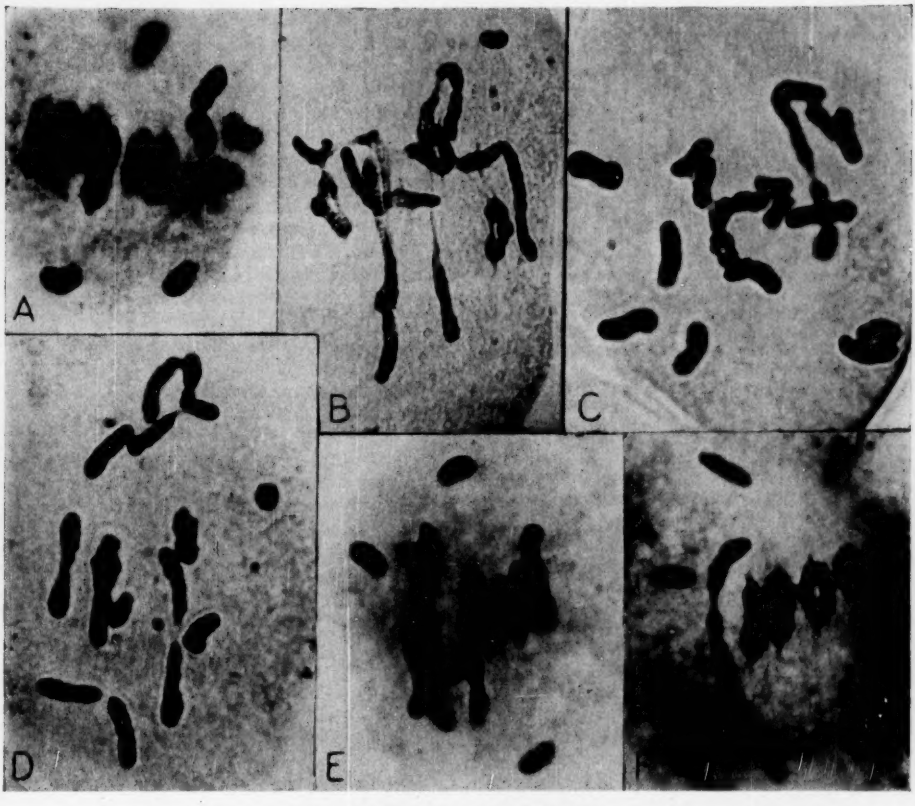
It is apparent from the data summarized in Table III that a high degree of homology exists between at least some of the members of the different chromosome sets, since the majority of the microsporocytes contained one or more multivalents—either trivalents or a



MEIOSIS IN BARLEY HYBRIDS

Figure 5

A—Metaphase I of *Hordeum sativum*. *B* and *C*—Metaphase I of *H. bulbosum*. *D-G*—Metaphase I of hybrid *Hordeum sativum* × *H. bulbosum*. *H*—Anaphase I of the hybrid. Note especially the dividing univalents. *I*—Anaphase II of the hybrid showing lagging chromosomes. *J*—Spore quartet with micronuclei. *K*—Pollen of *Hordeum bulbosum* and *L*—pollen of *H. sativum* stained rather lightly with aceto-carmine. *M*—Pollen of one of the hybrids showing varied stainability of the hybrid pollen with aceto-carmine. Magnification: *A* ×753, *B* ×867, *C* ×887, *D-J* ×867, *K* and *L* ×66, and *M* approximately ×66.



DISTURBED MEIOTIC PAIRING

Figure 6

Abnormal metaphase I figures observed in sporocytes of hybrids of *H. sativum* × *H. bulbosum*. Noteworthy features: *A*—atypical bivalent; *B* and *C*—extreme stickiness of chromosomes; *D* and *E*—sticky chromosome ends and centromeres; *F*—quadrivalent with univalent attached to probable centromere region of lower member. Magnification: *A* to *E* ×753 and *F* ×867.

quadrivalent plus a varying number of trivalents.

Fertility of the Hybrid

Stainable pollen was observed in all of the hybrid plants that were examined cytologically, although the amount varied with different plants and in different samples from the same plant. Stainable pollen from plant No. 32-7, Bolivia × *H. bulbosum*, varied in different samples from about 5 percent up to 23 percent, whereas in plant No. 26-6, derived from Wong × *H. bulbosum*, the amount of stainable pollen varied from approximately 6 percent to 11 percent. These data were based on observations of more than 1,000 cells of each plant. Common barley was pollinated with pollen from several of the hybrids, but no seed was obtained in spite of the fact that as many as 23 percent of the grains were well filled with starch and otherwise normal in appearance. No effort was made to determine cytologically whether the pollen of the hybrid was capable of germination. Seed has not been produced on any of the hybrid plants, and there was no evidence that self-fertilization

had taken place in any of the florets. However, it was usually observed that the anthers of the hybrids were extruded from the flowers as in the wild parent species, but they failed to open, presumably due to the high degree of pollen sterility. An exception to the typical behavior described above was noted in plant No. 32-7, which occasionally produced up to 23 percent stainable pollen. The anthers of this plant were sometimes observed to swell and open after being extruded from the flowers.

The reciprocal cross with common barley was attempted with the hybrid as the seed parent. The flowers of the hybrid were observed to open normally and the stigmas appeared to be receptive. When common barley pollen was applied to flowers on several hybrid spikes, it was noted that in one case two seeds started to form on one of the spikes. This spike was accidentally destroyed within a few days after it had been pollinated. A limited number of additional pollinations made later gave negative results. However, the possibility is not excluded that progeny could be obtained from larger numbers of pollinations together with the subsequent use of the embryo culture technique.

Discussion and Conclusions

The difficulty in obtaining hybrids of *H. sativum* and *H. bulbosum* has been due in the past to the early abortion of the developing seeds and their failure to germinate under normal conditions. With the aid of the embryo culture technique it is possible to provide a physiological environment favorable to the continued growth of the embryos and their development into viable seedlings.

Many of the immature hybrid seeds developed for as long as 15 days after pollination. The rate of growth was somewhat slower in the hybrid than in the seeds of cultivated barley. All but a very limited number of the hybrid embryos failed to develop into normal plants when placed on the culture medium at about 15 days after pollination, although non-hybrid embryos of the same age grew normally when cultured in the same manner. Apparently some unusual physiological condition inhibited the growth of the developing hybrid seeds.

Embryos originating from the same cross and developing in the same spike that were similar in size and appearance at the time of excision frequently differed markedly in the amount of growth and degree of development attained after transfer to the culture medium. This suggests that different genetically-controlled developmental reactions were involved, since the culture medium provided a very uniform environment for the growth of the embryos, and since there was no evidence of mechanical injury of the embryos during transfer.

The cultivated varieties of barley used in this study have 14 somatic chromosomes, the *H. bulbosum* parent has 28, and there were 21 chromosomes in the hybrids. All of the hybrid plants obtained in this study resembled the parent contributing the greater number of chromosomes more closely than the other parent, although there were differences between the hybrids and certain characteristics were intermediate.

The manner in which the hybrids were obtained is of particular interest since hybridization was achieved only when the plant with the lower chromosome number (*H. sativum*) was used as the pistillate parent. This is somewhat unexpected since most cross-compatible cereal species that differ in chromosome number have been hybridized more readily when the species with the higher number was used as the pistillate parent.

Meiotic chromosome behavior was normal in the varieties of *H. sativum* used as parents in the crosses. These varieties are diploids with seven pairs of chromosomes. The autotetraploid nature of the *H. bulbosum* parent was indicated by the prevalence of quadrivalents in the microsporocytes. The hybrids exhibited typical synaptic associations of the chromosomes as bivalents, univalents, trivalents and an occasional quadrivalent. In addition, in some cells there was more than the usual amount of stickiness of centromeres and chromosomes.

The bivalents observed in the hybrids could have resulted either from autosynapsis of *H. bulbosum* chromosomes or from allosynaptic associations of *H. bulbosum* and *H. sativum* chromosomes. Or, partly auto- and partly allo-synaptic

associations might also have occurred more or less at random. The last mentioned alternative is most probable in view of the prevalence of trivalents in many of the sporocytes, and the occasional presence of a quadrivalent.

There were one or more trivalents in 788 of the 1186 cells that were examined, a frequency that was definitely indicative of relatively close homology between the *H. sativum* and *H. bulbosum* chromosomes. In this hybrid the *H. bulbosum* parent contributed two sets of chromosomes which were free to pair *inter se* and thus satisfy the tendency of chromosomes to form pairs. The occurrence in the hybrid of trivalents involving chromosomes of both parent species is therefore indicative of closer homology between the *H. sativum* and *H. bulbosum* chromosomes than would have been indicated by the formation of bivalents if the parents had each contributed only one set of chromosomes.

Trivalent associations were more frequent in the hybrids derived from the varieties Wong and Bolivia than in those derived from the variety Moore. This is especially noteworthy since these same varieties crossed more readily with *H. bulbosum* than did the variety Moore. In other words, there was a positive correlation between frequency of trivalents in the hybrids and crossability of the parent varieties with *H. bulbosum*.

The occurrence of a quadrivalent at metaphase I in a number of cells of the F_1 hybrid can be explained most readily on the assumption that a reciprocal translocation was present in the homozygous condition in *H. bulbosum*, and that this translocation was not present in the varieties of *H. sativum* from which the hybrids were obtained. On this assumption the quadrivalent represents not the ordinary synaptic association of four homologous chromosomes but rather a translocation ring or chain of four chromosomes. A configuration having a chain of four instead of a ring of four appeared most frequently. This configuration was so similar in appearance to known interchanges involving one long and one short segment that the correctness of this interpretation can scarcely be doubted. Furthermore, on the basis of this assumption an occasional configuration of five or even six chromosomes would be expected, since the *H. bulbosum* gametes contributed two translocated chromosomes of each kind to the hybrids. Pentavalent associations have been seen but they occur very rarely.

The frequency with which the quadrivalent translocation complex was formed in the triploid hybrids can be used as an index of the frequency of allosynapsis in these hybrids, since such configurations must involve associations of two *H. sativum* chromosomes and two translocated *H. bulbosum* chromosomes. Autosynapsis of the two pairs of translocated *H. bulbosum* chromosomes present in the hybrid would produce two bivalents rather than a multivalent chromosome.

The formation of a translocation complex would be expected with a somewhat lower frequency than the formation of allosynaptic bivalents since the former includes four rather than two units, and the persistence of synaptic union between rather short homologous segments would be required for the translocation complex to be present at late prophase or metaphase I as a ring or chain of four chromosomes. However, the presence in the hybrid of two of each kind of translocated chromosome increases proportionately the probability that translocation complexes would be formed. The observed frequency of cells with a quadrivalent complex was 42 in 1186 cells, as shown in Table III. There was never more than one quadrivalent in any of the cells that were examined. Apparently, the parent species differed by only one translocation.

The degree of homology between chromosomes of the two species indicates that it should be possible to transfer desired characters from the wild to the cultivated species. More studies on crossability of the hybrids will be necessary before this can be ascertained. In addition to further tests of crossability involving other types of the tetraploid *H. bulbosum* it would be highly desirable to obtain the diploid form of that species for crossing with various cultivated varieties.

The synaptic behavior of the chromosomes in the hybrid plants was indicative of relatively close homology between the chromosomes of the parental species. However, the hybrids were highly sterile and no offspring have been obtained from them. This suggests that genic sterility as well as partial chromosome incompatibility and irregular disjunction may be involved.

The presence of self-sterility factors in the naturally cross-pollinated species *H. bulbosum* is indicated by the fact that Lein[4] obtained some seeds from plants of the tetraploid form but no seed on plants of a diploid form when each was selfed. In view of this evidence, it seems probable that a variety of cultivated barley having a genotypic constitution that will effectively inactivate these self-sterility factors in the hybrids may be required to obtain advanced generation progeny.

Summary

Hybrids of common barley, *Hordeum sativum*, and the wild species, *Hordeum bulbosum*, were obtained with the aid of the embryo cul-

ture technique. Eight of the 11 hybrids produced were studied cytologically, and there was evidence of relatively close homology between the chromosomes of the two species. There was a direct correlation between the frequency of cells containing multivalents at metaphase I in the F_1 progeny and the seed set on varieties of common barley crossed with *H. bulbosum*. No seed has been obtained from the hybrids, or from a limited number of backcrosses to common barley. This was true in spite of the presence of as much as 23 percent stainable pollen and normal-appearing ovules in the hybrids. It is suggested that the sterility of the hybrids may have been due in part to the expression of self-incompatibility genes present in the wild species.

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One Deer's Meat

To the Editor:

THE following is the story of "Bambi," the meat-eating deer. The fact that a typically herbivorous animal might develop a meat-eating habit by being reared by a dog would seem to raise some problems of interest to the geneticist, the physiologist and the enzyme chemist.

Workers on a banana plantation in the State of Yaracuy caught the deer, a female, which at that time might have been 15 days old. The animal was brought to the home of Mr. Marcel Monfils, director of the plantation, in Puerto Cabello, where she was immediately adopted and nursed by one of Mr. Monfils' dogs. Five weeks before, this dog had given birth to a litter of seven or eight, of which all but one had been taken away from her.

Bambi (that is the name of the deer) stopped suckling after about four months, but already after two months she started to develop strange eating habits, including a definite taste for meat.

Bambi is now about eight months old and eats everything: fruits, vegetables, herbs, bread, cigarette butts, clothes and furniture upholstering. But she is particularly crazy about meat, raw and prepared, and about fish. She will crunch chicken bones exactly like a dog. Once a bone got stuck in her throat but was promptly brought down by massaging.

Bambi is fond of all kinds of beverages, such as coffee, coca-cola, beer, liquors, etc.

Bambi has generally been in good health. However, nine weeks ago, she became slightly sick, lacking an appetite, slavering, and appeared to be in a depressed mood. But after only a few days she recovered completely and resumed her "normal" eating habits.

Pierre Budowski
Instituto Nacional de Agricultura
Maracuy, Venezuela

INBREEDING IS AGAIN IN FAVOR IN SOVIET RUSSIA

C. SOROKIN*

AS a method of plant and animal breeding, inbreeding has been in bad repute with the New Soviet Biology for two reasons. First, it was proposed, developed, and proved by Mendelists-Morganists. Second, it was condemned for not having given practical results, or at least as rapid results as expected. Just as everything else in the New Soviet Biology, the attack on inbreeding was started by the boss.

As early as 1935 Lysenko proclaimed that "inbreeding of a cross-pollinated plant always leads to biological impoverishment of hereditary constitution and therefore to the reduction of biological adaptation."[2] The work of Plachek on inbreeding in sunflower, and that of the Sugartrust on inbreeding in sugar beet, was particularly criticized and the following conclusion was drawn: "People stick to inbreeding for many years, for tens of years. In my opinion, uselessly, because of what use is the breeding work, if the hereditary constitution is wasted by inbreeding."[2]

Many plant and animal breeders who, even after the above evaluation of inbreeding by Lysenko, continued their work on inbreeding, and who did not want or did not know how to conceal their opinions and their work, paid for their persistence with loss of their positions and some of them with loss of freedom and ultimately with their lives.

The campaign against inbreeding has been under way since then. At the notorious session of the Academy of Agricultural Sciences of the U.S.S.R. in Moscow, from July 31 through August 7, 1948, Professor S. G. Petrov denounced Academician Serebrovsky for advocating inbreeding in poultry,[3] and N. I. Feiginson, speaking on inbreeding in corn, asserted that "Morganists proposed only certain intricate technical methods of obtaining such corn seeds (preliminary self-pollination and selection of self-pollinated lines), which were very difficult to apply on a mass scale."[1]

But, as dialectic teaches us, "everything is flowing, everything is changing." In 1950 the periodical, *Agrobiologiya* edited by Lysenko and dedicated largely to spreading his ideas, published an article by B. P. Sokolov entitled: "The Increase of the Effectiveness of Breeding Work in Corn."[4] Here we read: "It is difficult and it requires a long time to achieve a considerable change in the hereditary constitution in regard to the increase in productivitity (especially in the main corn producing regions where improved varieties are grown) by the methods of mass and group selection. Here other, more efficient methods of breeding, particularly hybridization with utilization of the first generation of intervarietal and interlinear hybrids, are necessary."[4]

Then we read that criticism of inbreeding was correct because geneticists and breeders "tried for many years in vain to obtain productive self-pollinated lines of sunflower, rye, sugar beet, corn and other crops."[4] "But does it mean that we must entirely refrain from inbreeding, and to discontinue the work on production of self-pollinated lines of corn? No, it does not mean this. This work should go on, taking into account the great effectiveness of the first generation after a crossing of self-pollinated lines." "Self-pollination of corn produces, under certain conditions, forms (lines) with hereditarily constant, economically useful characteristics."[4]

One can judge for himself to what extent such statements agree with what Lysenko wrote in 1935. "Some people emphasized that by way of inbreeding it is possible to create, easily and quickly, forms resistant to a certain disease and to use these resistant, though biologically weakened forms, by way of hybridization. I cannot yet imagine how it is possible to increase the resistance against disease by way of inbreeding? Where has it been shown that a biologically weakened organism proved to be more resistant against disease than a healthy unweakened one? But even if we imagine that the more a plant is biologically weakened, the more it is resistant against certain diseases, what then can one do with it? In this case it would really be possible to create resistant forms by way of inbreeding. Let us assume that some workers have already succeeded in creating such forms. But if this is true, these forms are resistant

*The author is an escaped Plant Breeder who is presently at the University of Texas, Austin 18, Texas.

only because they are biologically weak. The question is asked: where will this resistance be, when this inbred strain is used in crossing with the vitality of the organism increased manifold? It is certain that in this way, together with the increase in the vitality of a new hybrid organism, the resistance associated with the weakness of the organism, will be lessened."[2]

This was the argument of the master. Yet, Sokolov has found: "Many lines, we obtained by way of selfing, became parents of hybrids adopted, or showed hopeful signs for certain regions."[4] Then it is stated that: "in comparative tests of intervarietal hybrids' with varietal-linear and interlinear hybrids the last named ones stood out by their productivity and other economic characteristics."[4] The meaning of the terms are as follows:

"intervarietal hybrids"—obtained by crossing two varieties (*not* inbred strains),

"varietal-linear hybrids"—produced by crossing a certain variety with an inbred strain, and

"interlinear hybrids"—obtained by crossing inbred strains.

The following is a part of Table II on page 40.[4]

Productivity of Intervarietal, Varietal-Linear, and Interlinear Hybrids.

Year	Name of hybrid and variety	Yield in centner/hectare
1940	Stepniak-B-907 × G-380 (interlinear)	42.2
1940	Browncounty × Grushevskaia (intervarietal)	35.6
1940	North Dacota × C-84 (varietal-linea)	40.3
1940	North Dacota × Sterling (intervarietal)	35.9
1940	Dnieprovski-G-28 × C-84 (interlinear)	39.8
1940	Grushevskaia × Sterling (intervarietal)	35.4
1940	Browncounty (standard)	34.3

"The data of State trials on productivity of interlinear hybrids: Progress, Dnieprovski and Stepniak, in comparison with intervarietal hybrids and with parent varieties, prove that the best interlinear hybrids of corn surpass in the first generation both parental varieties and intervarietal hybrids."[4]

". . . neither we nor other breeders obtained good intervarietal hybrids from varieties belonging to the same botanical group. Self-pollinated lines behave in crosses quite differently. Even from close related varieties it is possible to create such diverse lines that they will give in the first generation a great effect despite the fact that they belong to the same botanical group."

"Numerous investigations together with the results of the State trials proved that the greatest increment in yield with the minimal expenditures occurs if hybrid corn seeds are sown. Best hybrids adopted for certain regions give on the average for several years in the first generation an increase in productivity up to 20 percent, and some of them in certain years up to 30 percent and even more as compared with the standard."[4]

However only two years ago one of the Lysenkoists, Feiginson, Scientific Director of the Mordovain Plant Breeding Station, asserted at the August session of the Academy of Agricultural Sciences that the method of production of hybrid seeds "suits the interests of capitalist seed firms, since in capitalist countries the methods proposed by the Morganists are beyond the capacity of the ordinary farmer."[1]

Who, then, is right, Feiginson or Sokolov, who two years later states that "the additional labor spent on growing hybrid seeds is comparatively small. According to our calculations, an increment in yield up to 25 centners corresponds to one working day. There is no other method which will be so profitable as the growing of hybrids of the first generation."[4] And a little farther: "The State Board on Variety Trails possesses vast material on trials of corn hybrids of the first and of the following generations."[4]

The question naturally arises whether this vast material on trials, not only of the first but also of the following generations of corn hybrids, was gathered by the State Commission overnight, or if all these data were well known to the President of the Academy of Agricultural Sciences, Lysenko, to the Scientific Director of the Mordovian Plant Breeding Station, Feiginson, to Sokolov, who possibly attended that session of the Academy, as well as to any of the plant breeders present at the session.

Poor Vavilov in his defense against Lysenko's attack on inbreeding was able to say in 1935 that about five percent of corn acreage in the U. S. was sown by hybrid seeds. He did not live to see that practically the whole corn belt acreage in this country is now occupied by corn hybrids. Though, if he had, he might have been answered by Lysenko as he was answered in 1935: ". . . I did not find in the literature (maybe, I do not know all of it) the confirmation of that figure, five percent of corn acreage sown in America with hybrid seeds obtained from crosses of inbred lines."[2]

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DONALD WALTON DAVIS

February 25, 1882 — June 30, 1950

Dr. Davis at Starved Rock Park, Illinois in 1939.

"I HAVE desired to contribute to the knowledge of my special field and to educational practice; to add appreciably to the welfare of my community; and to enjoy life with my growing family." Thus Donald Walton Davis wrote about himself in the twenty-fifth anniversary report for the Harvard Class of 1905. When on June 30, 1950, at the age of sixty-eight, Doctor Davis died from a heart attack, his fellow-citizens of Williamsburg, Virginia, his associates at the College of William and Mary, and many of his students, past and present, knew that he had satisfied those desires well.

Since 1916 — except for the period (1917-1919) during World War I when he served as first lieutenant of infantry — Doctor Davis was continuously at William and Mary as Professor and Head of the Department of Biology. For many years before his death he had been the senior member of the faculty. Always, over the years, he was diligently active in research, in teaching, and in community and civic affairs. And he greatly influenced the advancement of

science in the State of Virginia. As survivors he left his wife (who like himself is a native Pennsylvanian), two daughters, a son, and six grandchildren.

Before he joined the faculty of William and Mary, Davis had undergone a breadth of training and had experience which afforded the bases for his choice of genetics and marine biology as the two scientific fields in which he was chiefly interested. He attained from Harvard College the degree of A.B. in 1905 and from Harvard University the degree of Ph.D. in 1913. His affiliations with academic and scientific institutions are given below.*

In the early years of the century, bebefore genetics had come to stature, Davis became interested in this field of biology. At Harvard he was under the influence of Castle and East. And there he was the first doctorate student under Professor Herbert W. Rand. For his thesis Davis undertook at Woods Hole a study of *Sargartia luciae* (a marine coelenterate) in the expectation that the project would be genetical; it evolved, however, into a problem in regeneration (See *Journal of Experimental Zoology*, 1919).

Genetic Researches

Later Doctor Davis selected *Impatiens balsamina* for genetic study. This plant proved to be excellent material and well-suited to the hot summers of Williamsburg, Virginia. Prior to his return to the United States from Europe for discharge—to become captain, Cavalry Reserve — from the armed forces, he worked for several months in 1919 with Bateson at the John Innes Horticultural Institution and there made interspecific hybrids of *Impatiens*. At William and Mary, whenever his many duties would allow, Professor Davis grew balsams. His vigorous activity in his experimental plots was a subject for community discussion. (As likewise, until his death, were his tennis playing and his bicycling.)

All told he raised several hundred thousand plants. The day before his fatal heart attack he spent in the greenhouse with his seedlings. He determined the hereditary behavior of many characters, relating to flower color (discussed in manuscript), spur shape, plant stature, and photoperiodicity, and for some characters established linkage relations. Unfortunately, he published very few of his balsam discoveries. Most of the data remain in his notebooks, which are models of neatness and clarity. And if he were careful with his notes, he lavished attention on the plants themselves. Rarely are experimental gardens so well laid out as his were.

Marine Biology

The interest of Doctor Davis in marine biology reached back into his early years spent in California and at Woods Hole. Naturally, therefore, when he moved to the Virginia Peninsula, he was at once fascinated with the research potentials and problems of the area and with the need for the study of the fisheries of the James and York rivers and of the Chesapeake Bay. In the nineteen twenties he was therefore actively promoting the idea of a marine laboratory to be affiliated with the College. Finally, at his instigation and with assistance from other interested individuals, such an institution was established in 1940: the Virginia Fisheries Laboratory, jointly operated by the College and by the Commission of Fisheries of Virginia. At the very time of his death the Laboratory was being moved into a new and well-equipped building at Gloucester Point on the York River. That building is, in a sense, a monument to Doctor Davis as founder of the Laboratory.

He was also one of the founders, in 1923, of the Virginia Academy of Science and became its fifth president. He was ever a constructive force in the Academy.

His Influence as a Teacher

Significant though his promotion of scientific work was, Doctor Davis perhaps exerted most influence as a teacher—in the classroom and outside. No person of whatever age or background ever found him too busy to give enthusiastic instruction about a natural history specimen. At all times he was ready to apply his knowledge to problems—big or small —of the world about him. Accordingly, he was often a sympathetic participant in the problems and interests of other people.

For many years his experimental plants af-

*Assistant in Zoology, University of California, 1905-1906; Naturalist, Marine Biology Association of San Diego (now the Scripps Biological Institution), Summer, 1906; Graduate Student, Columbia University, 1906-1907 (also Teacher, Paterson, New Jersey, High School); Scientific Assistant, Woods Hole Laboratory, U. S. Bureau of Fisheries, Summers, 1904, 1905, 1907, 1908, 1909; Professor of Biology, Sweet Briar College, 1907-1909; Graduate Student in Zoology, Harvard University, and Instructor in Zoology, Radcliffe College, 1909-1912; Assistant Professor of Zoology, Clark College, 1912-1914; Professor of Biology, Depauw University, 1914-1916; Professor of Biology, College of William and Mary, 1916-1950.

forded William and Mary students their only opportunity to see scientific research in progress. His contagious excitement about those plants and his rigorous course in genetics stimulated a number of students to begin graduate study in biology. The nature of the William and Mary curriculum, however, caused more of his students to enter medicine than any other advanced field. To him many doctors are indebted for their basic premedical training.

As a formal teacher, he was probably at his best in the laboratory of the introductory course in biology. He never tired of seeing the same organisms year after year, and to him seeing was always an adventure. The better students caught the spirit of his teaching and wished to see and to understand for themselves. In every way that he could, he fostered independent work and original thinking. Whether good or poor, his students were privileged to untold demands upon his out-of-class time; and therefrom lasting friendships often developed.

Teaching Methods

Professor Davis was much concerned with teaching methods and techniques. Some were excellent; the philosophy back of all of them was sound. For example, he devised a means for keeping alive in the laboratory for several days an assortment of marine animals to be studied by the freshman student. Because he wanted the beginning students to learn to observe living things, he required them to collect insects and to take notes on them. So it was that students with insect nets came to be an expected part of the fall picture at William and Mary.

During the administration of four presidents at the College, Professor Davis continuously gave firm expression to what he believed in. He well deserved to be called the "most courageous member of the faculty." Stubborn wholesomeness was the essence of his character. He exemplified integrity, forthrightness, and honesty. He stood for high principles and sound scholarship: these, he would not compromise. He was a strong supporter of the principles of the Honor System and always insisted that they be properly observed. He devoted himself untiringly to Phi Beta Kappa and, when he died, was the local executive officer of the William and Mary chapter. He took great pride in the fact that Phi Beta Kappa had its beginning at the College. He was active in the American Association of University Professors and was a member of the council (1941-1946). As a matter of professional duty, he maintained membership in a number of scholarly and scientific societies and organizations, notably A.A.A.S., Botanical Society of America, Genetics Society of America, American Genetic Association, Virginia Academy of Science, Sigma Xi.

Doctor Davis likewise found time to engage actively in civic affairs. He was long a vestryman of Bruton Parish Church and for many years senior warden. He was one of the charter members and always a loyal supporter of the local post of the American Legion, in which he held a succession of offices. He devoted considerable time to scout work and advanced the cause of summer camps. To many worthy developments in his community he gave freely of himself. Seclusion in an academic world was not congenial to his nature. Men of training and character have a responsibility to impress themselves diversely upon society, and surely Donald Walton Davis did that well.

J. T. Baldwin, Jr.
College of William and Mary

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GENETICS OF POULTRY BROUGHT UP TO DATE

THE domestic fowl and its eggs are one of the important agricultural resources of the United States with an annual value of about three billion dollars. Of more direct concern to most geneticists will be the fact that the domestic fowl has been an important experimental animal from the very beginning of interest in Mendelian genetics fifty years ago. Hence, geneticists and others who use the domestic fowl as an experimental animal, as well as poultry breeders, will find much of interest in this new book on the genetics of the fowl.

Professor Hutt introduces the subject with a brief discussion of the origin and classification of birds followed by a somewhat more detailed discussion of the genus *Gallus*, the domestic fowl and its breeds. This is followed by a brief but adequate chapter on the cytology of the domestic representatives of this genus.

A large part of the book is devoted to the genetics of and variation in the skeleton, skin, plumage, color of the skin, color of the plumage with additional chapters on lethal genes and linkage. The seven chapters devoted to

**Genetics of the Fowl.* F. B. Hutt. McGraw-Hill Book Company, Inc. New York. 1949 XI + 590 pages, $6.50.

these topics come about as close as can be to an adequate, factual and well balanced discussion of the numerous items dealt with. They are not complete in the sense that everything known about the genetics of variation is mentioned, but this is to be expected since the author states in the preface that some "culling" has been done.

The chapters on variations in body weight, egg production, and eggs are written in the same thorough manner. The contribution of statistical methods to the description of these characters and to the problems of the improvement of these economically important characters is neglected. Otherwise the ground material is excellent and the appraisal of the work done by different investigators is sound. The contributions of heredity and environment are fully dealt with and their interaction is recognized throughout. The discussion of egg production is particularly complete. Professor Hutt decries the attempt to fit observations on such quantitative characters into Mendelian ratios and to explain them on the basis of one or two pairs of genes. The alternatives are not more fully explored within the framework of this volume. Perhaps this is as it should be.

Of particular interest to poultry breeders and poultry geneticists will also be the chapters on genetic resistance to disease, genetic aspects of reproduction, and genetics in practice. For the geneticist there are given in the appendix symbols for the genes of the fowl. Many of those who have worked with the fowl, including the reviewer, have not bothered to assign symbols to some of the genes reported. Professor Hutt points out that the same symbols have been used several times. He therefore undertook to assign symbols to those variations "clearly caused by the action of one pair of genes" using as a guide the recommendations of the International Committee on Nomenclature for Genetics of the Mouse (*Journal of Heredity* 31:505-506. 1940.). This section should prove useful, regardless of any disagreements about details.

For the student there is a glossary of genetical terms. The book is profusely illustrated and there is an adequate author and subject index.

The book is, for the most part, written in a clear, direct, readable style. Many informal, even humorous statements, enliven the pages of the book, particularly in the chapters dealing with egg production.

Professor Hutt has been one of the most important contributors to our knowledge of the genetics of the fowl. He has done a commendable job of writing a book that should prove useful and stimulating to all who have any interest in poultry genetics or in poultry breeding.

V. S. Asmundson
University of California, Davis.

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Cytologia Continues Publication in Japan

American cytologists, cytogeneticists, and geneticists will be interested to learn that *Cytologia*, international journal of cytology, is still being published in Japan at irregular intervals of four numbers per volume. No. 1 of Volume XVI, dated December 1950, has just been published. Among other articles, it contains one on "The Mechanism of Mitosis Based on Studies of the Submicroscopic Structure of the Living State of the *Tradescantia* Cell," by Bungo Wada of the Botanical Institute, Faculty of Science, University of Tokyo. One of the later numbers of Vol. XVI is scheduled to contain a symposium "On the Mechanisms of Nuclear Division and Chromosome Arrangement" under the editorship of Dr. K. Fujii. Twelve papers will be included in the symposium by such well-known Japanese cytologists as K. Fujii, K. Yasui, T. Shimamura, and K. Wakayama.

As with other Japanese scientific journals, *Cytologia* faced great difficulties in publication during World War II and since that time because of paper shortages, lack of funds, and other unfavorable conditions that adversely affect scientific work in a seriously strained economy. Japanese cytologists have risen above these almost unsurmountable obstacles to continue their research and publish one of the finest scientific journals in the world.

Cytologia is still under the editorship of the venerable Dr. K. Fujii of the University of Tokyo, regarded by most Japanese as the Father of Japanese Cytology. The Editorial Secretary is Professor Y. Sinoto, while the Business Secretary is Professor K. Yasui. To those interested in subscriptions to *Cytologia*, the current price is $7.50 per Volume. Communications to the Staff should be addressed in care of the Botanical Institute, Rigakubu 2-go-kan, University of Tokyo, P. O. Hongo, Bunkyo-ku, Tokyo, Japan.

Warren H. Leonard
Colorado A & M College
Ft. Collins, Colorado

"DWARFISM" IN ABERDEEN-ANGUS CATTLE*

MARVEL L. BAKER, CECIL T. BLUNN AND MOGENS PLUM
University of Nebraska Agricultural Experiment Station

DWARF calves are produced with considerable frequency in the three major beef breeds in this country. Whether all manifestations of dwarfism among the three breeds of cattle result from the same gene is not presently established. Observed phenotypic differences, however, indicate that several genes may be responsible although it is possible that the differences arise because of varying degrees of expression of the same gene, or because of the presence of modifiers.

In a previous paper, Baker, Blunn, and Oloufa[1] described dwarf calves designated as "stumpy" produced in a Nebraska purebred Shorthorn herd. From the analyses of the data presented it was concluded that the syndrome was caused by a single autosomal recessive gene. The present paper discusses certain data on the occurrence of dwarf calves obtained from the records of a purebred herd of Aberdeen-Angus cattle, also in Nebraska.

These Angus dwarfs differed phenotypically from the "stumpy" Shorthorn calves previously described, for at birth they were not always readily distinguishable from normal calves. At varying ages, from birth to an age of two or three months, they usually exhibited exceptionally compact, low-set, thick bodies, with short, wide heads. Most of them also exhibited a higher degree of finish or condition than did the "stumpy" Shorthorn calves. A dwarf calf is shown in Figure 8. However, they usually did not gain and fatten normally and after a few months did not show the same thickness and degree of finish as they had at an earlier age. The head also appeared relatively longer and narrower than at an earlier age. Individual weights were available in only a few cases. One calf weighed 280 pounds when 190 days old; a second one 380 pounds when 278 days old; and a third 630 pounds at seventeen and one-half months. No dwarf calves died in the herd. Bull and heifer calves were produced in approximately equal numbers.

Dwarf Angus calves similar to the calves observed in this herd have been observed by the senior author in other Angus herds in Nebraska and in one other state, while verbal reports from different geographic areas indicate the condition is fairly common. All of the evidence indicates that the frequency of dwarfism is increasing rapidly, as would be expected if the heterozygotes were preferred by feeders over the homozygous normal animals because of their phenotypic appearance.

Data and Discussion

The Angus herd in which the dwarf calves under discussion appeared had been linebred to some extent at different periods for several years. However, as far as the herd records indicated, no dwarf calves were produced until February, 1941, when one dwarf calf was born. This calf was sired by *A*, a bull used in the herd from June, 1935 until May, 1941. During this period he sired a total of 64 calves of which 33 were daughters. Twelve of these were retained and added to the breeding herd. Two of these were mated back to their sire and one of them, *H*, produced the dwarf calf.

No dwarf calves were then produced until 1946 when three calves out of 31 were dwarfs. In 1947, three calves out of 26, and in 1948, three out of 22 were dwarfs.

Examination of the pedigrees of the dwarf calves produced in the three years revealed that in every instance they traced through both sire and dam to *A*. Two of them were from *H*, the daughter of *A*, which had produced the dwarf calf in 1941 when mated back to her sire. Another one was from *H-2*, a daughter of *H*. All of the nine calves were either by sire *B* out of dam *F*, a daughter of *A*, or by sire *C* out of dam *G*, also a daughter of *A*. *B* and *C* were by different sires. Pedigree analyses and the breeding performance indicated that neither of the sires of *B* and *C* carried the gene for dwarfism.

The dwarf gene is not sex-linked because phenotypically normal bulls and cows have been mated and almost equal numbers of dwarf bull and heifer calves have been produced.

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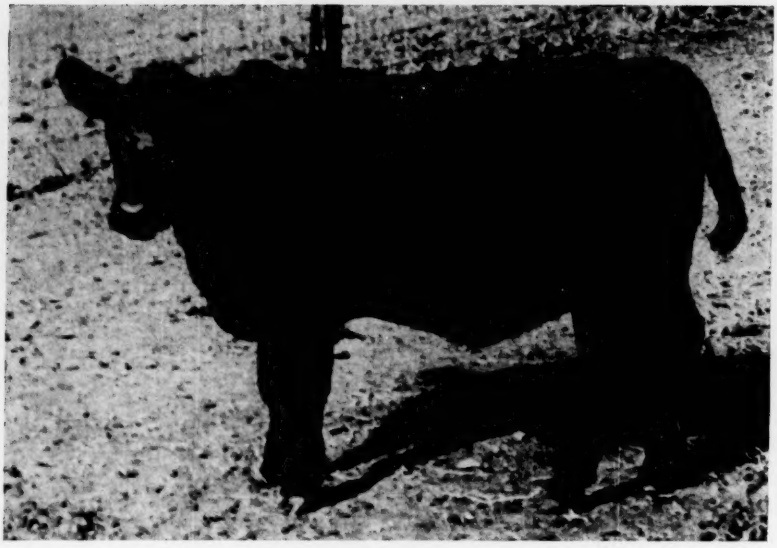

DWARF ANGUS
Figure 8

Nine dwarfs have appeared in an Aberdeen-Angus herd in an interval of eight years. A recessive gene appears to be the causative factor. There may be a tendency to select heterozygous individuals as breeders, but if it exists it is not very great.

The number of breeding animals involved in this study is small as shown in Table II. This fact, combined with the limited number of calves produced by each cow, makes it extremely hazardous to draw definite conclusions concerning the mode of inheritance of dwarfism. It is interesting, however, to see what some of the possibilities might be.

Seven cows have produced at least one dwarf calf and are therefore heterozygous. Two other cows are known to be heterozygous for they are the dams of bulls *B* and *C*. These nine cows have produced 16 normal and 9 dwarf calves. Since these cows have produced either two or three calves apiece, it is relatively easy to calculate the expected frequency of normal to dwarf calves. Following the method given by Li[4] which makes use of Lentz's correction the information may be displayed in tabular form (Table I).

The observed ratio in Table I is $\frac{9}{45.4671}$ or $\frac{1}{5.0519}$. The expected frequency of dwarf calves is $\frac{1}{4} \times \frac{45.4671}{25}$ or 0.4547. From this the expected ratio is 13.63 normal to 11.37 dwarfs. The χ^2 test shows that this ratio fits the observed ratio quite well ($0.5<P<0.3$) This is in support of the single gene hypothesis and agrees with the results of studies on the inheritance of dwarfism in other breeds.[3, 2, 1]

As stated previously, there is some evidence that the heterozygous animals might have been saved because of their phenotypic appearance. This would happen if the presence of a single dwarf gene gives the heterozygous animals a more desirable phenotype than those lacking the dwarf gene. In 1946, nine of the 12 daughters of *A* originally retained in the herd, were still in it. Six of these nine daughters have been definitely classified as carriers of the dwarf gene, for they either had produced a dwarf calf or had produced the heterozygous bulls *B* and *C*.

The data are meager, but they furnish a means of testing the hypothesis that selection

Table I. Expected and Observed Distribution of Dwarf Calves

Family size S	No. of families S_n	Total No. offspring SN_n	No. of dwarfs r_n	Theoretical total SN_n $1-(\frac{3}{4})^n$
2	2	4	1	9.1428
3	7	21	8	36.3243
Total	9	25	9	45.4671

was not in favor of the heterozygote. If the assumption of a single recessive gene is correct, tnen the production of one dwarf calf is all the evidence needed that an animal is heterozygous. On the other hand, the proof that the three remaining daughters of *A* which had no dwarf offspring are non-carriers is inadequate, being based on families of three.

The probability of daughters of *A* being homozygous (non-carriers) is ½. Since the average number of offspring from these daughters was 25/9 when mated to a heterozygous carrier bull the probability of these cows having only normal calves is:

$$\tfrac{1}{2}\ [1 + (\tfrac{3}{4})^{2.778}] \text{ or } 0.7248.$$

The probability of their having at least one dwarf is:

$$\tfrac{1}{2}\ [1 - (\tfrac{3}{4})^{2.778}] \text{ or } 0.2752.$$

Among the daughters of *A* the expected ratio between cows expected to give only normal calves and cows expected to give at least one dwarf offspring is 6.52 cows with only normal calves to 2.48 cows with one or more dwarf calves. The actual distribution was five to four.

The granddaughters of *A* are divided into two groups. First those which were from heterozygous dams and second those which were from dams not known to be heterozygous. Five granddaughters of *A* have known heterozygous dams. When mated to a known carrier tne probability of their producing at least one dwarf in a family of three is $\frac{1}{2}[1-(\frac{3}{4})^3]$ or 0.2891. The expected ratio for these five cows is 3.55 with no drawfs to 1.45 with dwarfs. Actually three have produced a dwarf calf while two have not.

Table II. Number of normal and dwarf calves produced from daughters and granddaughters of *A*, and sired by *B* and *C*, grandsons of *A*.

Dams	Normal	Dwarf
1. Daughters of *A*		
D	1	1
E	3	0
F*	3	0
G*	2	0
H	1	2
I	3	0
J	2	1
K	3	0
L	1	2
Total for daughters	19	6
2. Granddaughters of *A*		
E-1	1	0
F-1	2	1
G-1	3	0
H-1	3	0
H-2	2	1
I-1	3	0
J-1	2	1
K-1	2	0
K-2	3	0
Total for granddaughters	21	3

*F and G are carriers since they are the dams of the heterozygous bulls B and C.

The probability of getting dwarf offspring from a mating of the four remaining granddaughters of *A* to a known carrier is rather complex. These four granddaughters were from three daughters of *A* (*E*, *I*, and *J*) that produced only normal calves, but who had a probability of producing dwarf calves of .2752. In a large population the frequency for the dwarf gene among offspring of females with this gene frequency and carrier males (gene frequency ½) would be .2752. Since the evidence for this gene frequency is based on only three "families" of three offspring each, Lentz's correctjon must be again applied. Using Lentz's correction, the theoretical total of the three families becomes $9/(1-(\frac{3}{4})^3)$ or 15.567 giving an estimated gene frequency of 0.16. The probability of a granddaughter in this group producing a dwarf, therefore, becomes $0.16[1-(\frac{3}{4})^3]$ or 0.0925 in families of three. The expected ratio of non-dwarf to dwarf producers is 3.63 to 0.37. Actually the four granddaughters produced only normal calves. The χ^2 values for these tests are all within the range expected from sampling.

The most likely conclusion seems to be that the dwarf condition is governed by a single autosomal recessive gene. Although verbal reports seem to indicate that dwarf calves appear more and more frequently within the herd indicating that some selection for the heterozygous type might take place, the results of this study do not give any statistical support to the theory that such selection actually takes place.

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DEVELOPMENT OF ADVENTITIOUS BUDS

Figure 9

A—Stem of Giant Kimball McIntosh apple tree, with four adventitious buds (*a*, *b*, *c*, *d*). These buds were caused to erupt by decapitating the stem and killing the normal buds. Natural size. *B*—The same stem about a month later. A cluster of shoots has arisen from bud *a* and a single shoot from bud *d*, but the other two buds have remained inactive. The shoots from bud *a* proved to be diploid; that from bud *d* was tetraploid.

TETRAPLOID AND DIPLOID ADVENTITIOUS SHOOTS

From a Giant Sport of McIntosh Apple

HAIG DERMEN*

IN 1943 Mr. Roger Kimball of Littleton, Massachusetts, discovered on a McIntosh apple tree a centrally located branch bearing much larger fruits than the lateral branches. In succeeding years this branch continued to produce large fruits. Budwood from this "gigas" branch, presumably a sport, was obtained and grafts were made by W. H. Thies and W. E. Weeks of the Agricultural Experiment Station, Amherst, Massachusetts. In January 1948, we received from that station three one-year-old trees. These were kept in the greenhouse. Three other trees obtained later were set in the orchard.

An earlier report[8] described this sport. Smear preparations made at that time did not permit a final decision as to the nature of this sport. The present report is mainly based on observations made on the first three trees; the others were kept in reserve. The purpose of this study was: (a) to determine by a detailed cytohistological analysis of sectioned material the exact make-up of this sport, and (b) if it was found to be a diploid-tetraploid chimera, attempt to obtain entirely tetraploid shoots through the adventitious bud technique.[5]

One tree, No. 1, was allowed to grow shoots from normal buds. The other two trees, No. 2 and No. 3, were disbudded in such a manner as to induce the development of adventitious buds.[5]

A normal shoot tip from tree No. 1 was examined by the smear technique. It was found to be chimeral with a cytohistological constitution of 2-4-4,† the epidermis being diploid ($2X = 34$ chromosomes) and all other tissues tetraploid ($4X = 68$ chromosomes).[8] Thus it appeared that the large fruits of the "gigas" McIntosh were due to polyploidy of all internal tissues in that particular branch. Further evidence presented below establishes the fact that the initial change in this branch had been to a periclinal chimera with a tetraploid hypodermis (2-4-2). Later a second change must have produced branches having a 2-4-4 constitution.

Production of Adventitious Buds

Adventitious buds developed on both disbudded trees. On tree No. 2 only one adventitious bud developed, from which a cluster of shoots grew. On tree No. 3, four adventitious buds developed; these are marked *a*, *b*, *c* and *d* in Figure 9*A*. This photograph shows bud scars of six of the seven true buds that were distributed at definite nodal intervals along the stem. The adventitious buds *a*, *b*, and *c* are located vertically along one side of the stem, and bud *d* is slightly to the right, off the line of the other three buds. The same stem is shown in Figure 9*B*, reduced about half in scale, to show the branching in relation to the buds in Figure 9*A*. A cluster of shoots developed from bud *a*. No shoots arose from buds *b* and *c*; and one shoot arose from bud *d*.

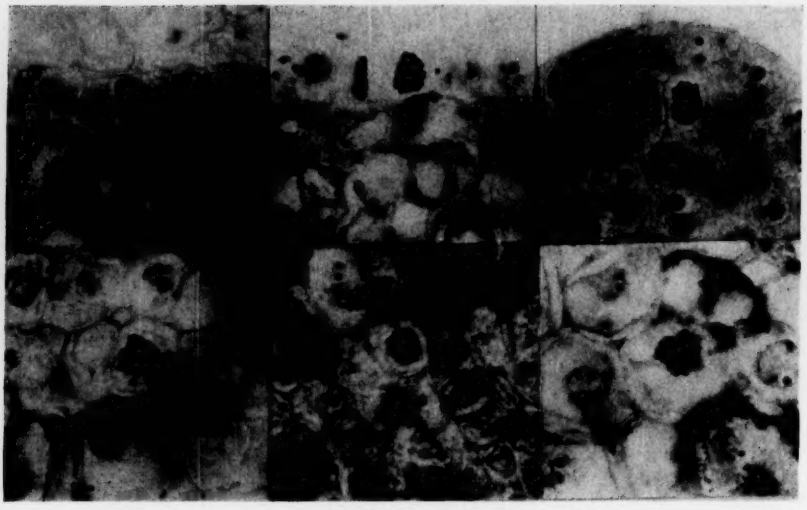
These trees had been planted and disbudded on January 23, 1948. On March 10 the first indication of adventitious swelling at bud *a* was noted. The stage of development shown in Figure 9*A* had occurred by April 23, and shoot emergence at bud *a* began on April 26. Figure 9*B* shows the situation on May 25.

For cytological study, shoot tip preparations

*Cytologist, Division of Fruit and Vegetable Crops and Diseases, Bureau of Plant Industry, Beltsville, Maryland.

This paper is appreciatively dedicated to Dr. George M. Darrow, president of the American Society of Horticultural Science, during 1949, because of his unbounded enthusiasm regarding polyploidy and its place in the breeding of fruits.

†In this paper the first numeral stands for the epidermis of the stem, the second for the hypodermis, or outer cortex, and the third for the remaining tissues—inner cortex, stele with the pith. See Literature references 2 and 5 for details.



DIPLOID TISSUE

Figure 10

Chromosome plates in the tissues of stems from bud *a* in Figure 9. *A-B*—*2x* plate in epidermis, in hypodermis (*C*), in cortical region (*D*), in stele region (*E*), and in pith region (*F*). Figure *A* shows a rare periclinal division in an epidermal cell. ×1000.

were made by the paraffin section method from two normal shoots of tree No. 1, from an adventitious shoot of tree No. 2, and from an adventitious shoot from bud *a* of tree No. 3 (Figure 9*B*). At the time this sampling was made, the shoot from bud *d* was growing quite slowly. It was considered not suitable for a thorough cytological determination of its ploidy status, and was left for later study.

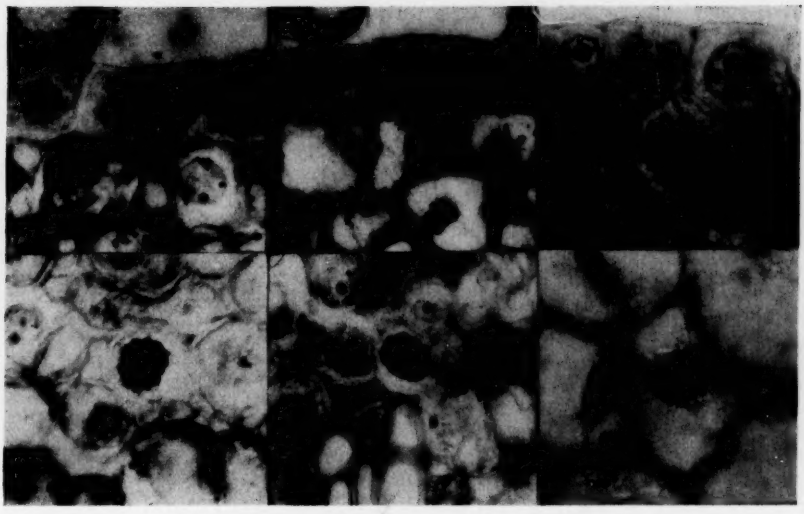
As previously determined,[8] tree No. 1 was found to have a 2-4-4 periclinal constitution. The samples from the other two trees upset our calculations. Both of these were found to be uniformly *2X* instead of *4X* as expected. This could be accounted for either by the assumption that trees No. 2 and No. 3 were diploid or that their chimeral constitution was 2-4-2. In either case adventitious shoots would have been entirely *2X*. This is because adventitious buds develop in the outer phloem,[5] *i.e.* the outer part of the stele system. When the apple has a 2-4-2 constitution the stele in the stem would be expected to be diploid. Tetraploid cells would be confined either to the hypodermis or to the outer cortical region.[9] Whether tree No. 2 had a 2-4-2 constitution could not be determined by the present study, since its growth consisted of only one adventitious bud from which a cluster of shoots developed, all of them being entirely *2X*. That tree No. 3 was mainly of a 2-4-2 constitution with a sector of 2-4-4 was indicated from the diploidy of shoots from bud *a* and from the fact that bud *d* was an entirely tetraploid shoot as shown below.

The leaves on the shoot developed from bud *d* remained small in size but were more round in shape than the leaves on the shoots from bud *a*. This suggested the remote possibility that the shoot from bud *d* might be tetraploid.

Stomate length measurements were made from leaf samples of tree No. 1, and from shoots derived from buds *a* and *d* of tree No. 3. The range and average of stomate length were as follows:

1. Tree No. 1: range (18 stomates) 26.5-33μ; average 28.5μ.
2. Tree No. 3: Shoot *a* (18 stomates) range 22-31μ; average 27μ. Shoot *d* (21 stomates) range 31-42μ; aver. 35.5μ.

These measurements suggested that shoot *d* was tetraploid. Similar measurements were made later on material from the same sources but of more vigorous growth (of whips obtained from budding). The differences in stomate size between the tetraploid and diploid leaves were not as much as shown above,



FULLY TETRAPLOID TISSUE

Figure 11

Chromosome plates in the tissues of the stem from bud *d* in Figure 9. *A-B*—4*x* plate in epidermis, in hypodermis (*C*), in cortical region (*D*), in stele region (*E*), and in pith region (*F*). A shows, as in Figure 10*A*, a periclinal division in an epidermal cell. ×1000.

which indicates that such measurements of themselves may not be relied on as conclusive evidence in the determination of ploidy of apple material.

On July 18, 1948, after shoot *d* had stopped growing, buds from it were grafted* into seedling apple stocks. All lateral buds (seven) were cut off for this operation, leaving only the stem with its terminal growth. The cuts were taped over and the shoot remained alive in spite of the severe injury. We had, during the summer and fall, six actively growing trees from this source. Tips from two of these trees were prepared by the paraffin method and examined. *The shoot from bud d proved to be tetraploid in all its tissues.*

The diploid chromosomal status† of the shoots from bud *a* of tree No. 3 is illustrated in Figure 10*A-F*. Here chromosome complements are shown for five different tissues. The tetraploid constitution of the same five different tissues of a shoot from bud *d* is illustrated in Figure 11*A-F*. All preparations are shown at the same magnification. Mitotic figures illustrated in Figures 10*A* and 11*A* are presented merely to show that in rare instances cell division in the epidermis may be in the periclinal plane, rather than in the usual anticlinal plane. This observation indicates that internal tissue development may at times occur from this source. This would permit the production of somatic chromosomal sports, including sectors or even whole branch systems. Such an event might change the status of the cytological or genetic make-up of parts of plants or even entire plants[2,3,4,7].

Discussion

In a number of recent publications the cytohistological and histogenic aspects of chimeras of a number of plants were discussed.‡

In one of these publications[5] the ad-

*The successful budding from this slender shoot was made by Dr. Paul Marth.

†Very seldom could chromosomal status be determined from actual counts; very often this had to be based on an estimate of the chromatine mass or nuclear size after accurate counts were made in a few cells.

‡See literature citations 1 to 8.

ventitious bud method of propagation from some apple varieties was shown. It was suggested in this article that by this method homogenous diploid or tetraploid shoots might be obtained from diploid-tetraploid chimeral plants. The experiment here described on a giant sport of McIntosh apple (which was shown to be a diploid-tetraploid chimera), is the first definite proof of the effectiveness of that technique. Thus, for the first time we have been able to obtain from adventitious buds an entirely tetraploid form of an apple variety. This technique offers promise for obtaining tetraploid forms from other diploid-tetraploid chimeras of other varieties.

The cytohistological constitution of the sport in this Kimball tree was first reported to be 2-4-4[8], but the present investigation indicates that it most probably occurred originally as a 2-4-2 chimera.* The chimeral condition in the innermost tissues in some portion of the tree must have changed from 2-4-2 into 2-4-4 or 2-4-4/2. The latter formula designates a sectorial (mericlinal) condition in a periclinal chimera in the tissues comprising the inner cortex and stele and possibly the pith. A sector of that tissue system would be 4*X* and the remainder would be 2*X*. Thus it may be assumed that of four buds on tree No. 3 buds *a*, *b* and *c* grew out from the 2*X* portion of the stele and bud *d* from the 4*X* sector of the stele. That this may have been the case is further suggested by the fact that the stem was thicker along the side where bud *d* appeared and shallower along the side where buds *a*, *b* and *c* were located. This is presumed to be due to the larger cell size in the tissue system in the stem on the side of bud *d*. It was indeed fortunate that shoots from buds *a* and *d* developed and afforded evidence of the underlying structure which determined the cytohistological pattern described here.

A Winesap Polyploid Chimera

Another polyploid-chimeral sport has been discovered; this in the Winesap apple. This was found by J. J. Reimer in his orchard at Palisades, Washington. Budwood from this tree was collected in 1932 by my colleague, C. P. Harley. Budded trees were planted in the orchard at Beltsville in 1934. The Reimer tree bore fruit showing great disparity in size, varying from very large, through intermediate to small. Some of the large and intermediate fruits were irregularly shaped. Some were quite round and others flat. The small ones were of regular shape. Some of the large fruits weighed twice as much as the normal fruits and measured approximately 3¾" in diameter and 2½" from stem to calyx.

A few years ago J. R. Magness called the writer's attention to this Winesap Sport. Its meiosis was studied and was found to be normal 2*X*. On August 10, 1949, in a good crop year, a number of buds were taken from branches bearing large fruits and were budded on rootstocks. By September 20 a bud had started to grow into a shoot. Its tip was prepared by the paraffin method and examined. It was found to have a 2-2-4 periclinal constitution, thus indicating that the increased fruit size of this Winesap sport was due to tetraploidy of the innermost tissue system consisting of the inner cortex, stele with the pith.

An intensive effort is being made to obtain from this Winesap chimera a homogeneous tetraploid form through the adventitious bud method. Should this be obtained another important apple variety would be added to the list of chimeral sports now available for breeding on a polyploid level. These sports are in the variety McIntosh, Ontario, Yellow Transparent, and Wealthy (the last three having been described by Einset and Imhofe[10]). All of these tetraploids are now available for breeding, so that a great many crosses may be made to produce triploid and tetraploid seedlings for selection of desirable types at a polyploid level. That crosses between a tetraploid and a diploid variety actually do yield a large percentage of triploid seedlings has only recently been tentatively confirmed by an examination of material supplied to the writer by E. M. Meader of the Agricultural Experment Station, Durham, New Hampshire.

These developments may be considered as ushering in a *new era* in the breeding of apples.

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*This was verified from one of the trees which had been left to grow in the orchard, after this article was submitted for publication.

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MULTIPLE GENES IN LIVESTOCK IMPROVEMENT

THE successful application of genetics to livestock improvement could not be attained until the preoccupation of genetics with unit differences due to single genes wore itself out and the inheritance of continuous variation became a serious part of genetical research. Genetics then moved from the laboratory to the study because the foundations of quantitative genetics had to be laid by mathematicians who could work out the statistical consequences of multifactorial inheritance. This approach was pioneered principally by Fisher, Wright, and Haldane. As a result of their work the genetics of quantitative inheritance was built into a substantial and coherent theory. But the emphasis was placed more on natural selection and evolution than on artificial selection and livestock improvement. The principles were, however, the same, and after interpretation and adaptation by Lush the theoretical deductions of "population genetics" turned animal breeding from an art into a science. Measurement and calculation could then replace guesswork in selecting as parents those individuals which were most likely to raise the genetic level of a population.

There has as yet been little time to prove the worth of the improved techniques of selection by their results, and a phase of experimental application is needed to establish the general validity of the deductions. Professor Lerner's pioneer work with the University of California poultry flock belongs mainly to this phase, and with the comparatively rapid breeding of poultry it has already made much progress. Professor Lerner is therefore very well qualified to write on this subject, and in this book* he shows how modern genetical theory can be applied to a selection project to increase egg production. This is not merely a manual of modern poultry breeding: it is also a text book of applied genetics with the illustrative statistical parameters supplied mainly from poultry. The first third of the book sketches the history of the application of genetics to poultry breeding and describes the biology of egg production and the management of the University of California flock. In the rest of the book the principles of applied population genetics are developed in general form—the fundamental postulates, the concept of heritability, systems of mating, selection indices, and much more besides—the whole subject being illustrated by its application to the improvement of egg production. This exclusiveness of illustrative material gives coherence to the whole and has the further advantage that at every point one knows the author speaks with authority. The reader inevitably acquires some familiarity with the biological material essential to the correct application of the theory; and this could scarcely have been achieved with a more general treatment. The author, however, does not hesitate to draw on other material when necessary and is at pains to stress the points at which poultry differ from other material, for example, in the absence of non-hereditary variation acting between family means. The widely felt need for a text book of applied genetics is, therefore, admirably supplied.

One of the most valuable features of the book is the emphasis placed on the incompleteness of our knowledge of quantitative inheritance. The need for experimental verification of theoretical deductions is frequently pointed out, and many suggestions for future experiments are made. The claim that Professor Lerner's selection for egg production provides one such verification, because the rate of improvement achieved agreed with predictions based on estimates of heritability, will however be regarded by some as over-confident. Those familiar with selection experiments on laboratory animals will recognize the usual erratic nature of the response to selection and will be more impressed by the magnitude of the sampling errors than by the actual agreement obtained. But there is no denying the improvement in egg production, and an experiment with an economic character in a domestic animal is of much greater practical

*LERNER, I. MICHAEL, *Population Genetics and Animal Improvement.* 342 pp. Cambridge University Press, New York, 1950. $5.50.

value than the best laboratory experiment.

The book is primarily addressed to "investigators, teachers and advanced students." It will be of very great value on account of the clarity of the presentation of a difficult subject, its stimulating ideas, and its collection of tables and formulae. It is published and printed by the Cambridge University Press and takes a worthy place among distinguished company in the 'Cambridge Biological Studies' under the general editorship of Professor C. H. Waddington. The printers are to be congratulated on the beauty of the lay-out, and the accuracy of setting of the many complex formulae.

D. S. FALCONER
Animal Breeding and Genetics Research Organization,
King's Buildings, Edinburgh, Scotland.

◆

WINGE ON INHERITANCE IN DOGS

A distinguished Danish geneticist, who has made important studies of inheritance in a wide variety of organisms ranging from yeasts to mammals, has published the most comprehensive account yet written of inheritance in dogs.* It is based largely on a study of records contained in stud-books of the Danish Kennel Club and was designed primarily for the information of dog fanciers having only a limited knowledge of the science of heredity. It is admirably suited for this purpose, and will be welcomed by breeders and fanciers of dogs the world over. The English translation by Dr. Catharine Roberts has been made with great care and the colored plates are excellent.

The book contains a large amount of useful information about the genetic constitution of various breeds of dogs and the results to be expected from crosses between them or between different color varieties of the same breed. But from a scientific standpoint the account is unfortunately confused and difficult to correlate with existing knowledge of the genetics of other mammals.

Early chapters deal with the dog as a domesticated wolf, with dog chromosomes, of which there are 39 pairs, known to be bearers of genes and functioning in the determination of sex. Other chapters deal with the formation of new breeds, the effects of inbreeding, and the fallacious idea of telegony.

In his use of genetic formula, the author introduces a useful convention which I shall follow here. When it is a matter of uncertainty and of no consequence whether a particular dominant gene is present homozygous or heterozygous, since in either case it will be equally effective, the symbol is written only once. But a recessive gene, in order to show its presence, must be homozygous. Thus, *Aee* in such a formula would indicate effective presence of gene *A* (either as *AA* or as *Aa*), as well as effective presence of recessive *e*, in the homozygous condition, *ee*.

Elementary Mendelism is explained by the author and illustrated in examples involving one, two and three character differences, viz., (1) black × brown, (2) black self × brown white spotted, (3) black self × brown white spotted and speckled.

It is worth noting that in these examples the author correctly designates black with the symbol *B*, and its recessive allele brown with the symbol *b*, but in later chapters he confuses the relationship describing *B* as a "(yellow) red factor," and *E* as a "brown factor, which in itself produces a brown coat." He states that "*B* + *E* produces a black coat through a complementary effect."

What he should have stated, as I think, was correctly formulated by Little and Jones.† They observed that *B* is a gene for black pigmentation, *b* for brown; that *E* is a gene effecting extension of black (or brown) pigmentation throughout the coat; that its recessive allele *e*, when homozygous, restricts distribution of black (or brown) pigmentation to eyes and skin, leaving the coat red or yellow.

Effective combinations of genes *B* and *E* are (1) *BE*, black coat, eyes and skin. (2) *Bee*, black eyes and skin, coat red or yellow. (3) *bbE*, brown coat, eyes and skin. (4) *bbee*, brown eyes and skin, coat yellow.

Winge's colored plates accord with this terminology, but his text in places contradicts it.

In a list of the genes of dogs, Winge introduces a hypothetical gene *C*, standing for self-colored-coat, in contrast to a series of black-red (or brown-red) color patterns. It seems to me more probable that the color patterns which he lists belong in the extension series, as suggested by Little and Jones. If we were to substitute *E* for Winge's *C*, his list would

*WINGE, O. *Inheritance in Dogs*, with special reference to hunting breeds. 153 pp., 5 plates. Comstock Publishing Co., Ithaca, New York, 1950. $3.00.

†LITTLE, C. C., and E. E. JONES. The Inheritance of Coat Color in Great Danes. *Jour. Hered.* 10:309-320. 1919.

become: E', E, e^{bl}, e^{br}, e^{sa}, e^{ma}, and I would add to it e. Dominance among these supposed alleles is stated to be substantially in the order given. If each of them occurred in association with B, the resulting phenotypes would be:

BE', dominant black, as in rabbits and the black rat, *Rattus rattus*; BE, recessive black, as in mammals generally; $Be^{bl}e^{bl}$, bicolor, black and tan; $Be^{br}e^{br}$, brindle, tan with black tiger markings; $Be^{sa}e^{sa}$, tan with black saddle, as in Airedales; $Be^{ma}e^{ma}$, tan with black mask on head; Bee, tan (yellow) with black eyes and skin, as in most other mammals.

In support of this interpretation, it may be stated that dominant black in rabbits has been clearly demonstrated to have arisen as a mutation in the extension gene. Also BE, recessive black, and Bee, restricted black (yellow), are well known and demonstrated phenotypes in a majority of mammals. Mosaic color patterns intermediate between BE and Bee are found in brindle guinea pigs and in the Japanese rabbit, as demonstrated alleles of E and e respectively.

Other mutant genes of dogs as listed by Winge are:

A, dominant red, epistatic to black or brown; seen in the Irish setter and in dachshunds.

d, blue dilution, recessive to black.

f, a recessive [pseudo] albino gene, "in *ff* animals all colors are bleached to such an extent that they are practically invisible, but eye color and nose color are unaffected"; "True albinos with red eyes are rare and are due to another recessive albino gene."

G, wild color gene. BEG is gray (wolf color), but $BE'G$ is dominant black (G being hypostatic to E').

H, harlequin, incompletely dominant to self black. Heterozygotes (*Hh*) in Great Dane and some other breeds have large or small roundish black spots on a white or grayish background. Homozygotes (*HH*) are inferior in markings or frequently defective, deaf or blind. Harlequin breeds are unfixable like the blue Andalusian fowl. Good specimens bred together produce on the average 1 black : 2 harlequin : 1 poor or defective specimen.

k, long hair is recessive to *K*, short hair.

L, short crooked legs is dominant over *l*, normal legs.

R, roan or dappled, produces dark speckling in white areas of white mottled dogs.

S, small speckled spots in white areas of white mottled dogs. Similar in effect to *R*. Produces "belton" effect.

t, recessive white mottling, seen in pointers and cocker spaniels.

W, wire hair dominant both to ordinary short and ordinary long hair.

z, recessive cinnamon factor, reduces the intensity of brown and red colors, when homozygous.

The author devotes several chapters to inheritance within particular breeds, which should be of much value to practical breeders, as the results to be expected in specified matings are described in detail and, in general, correctly, though the theoretical interpretations offered are in some cases questionable. I shall mention only one instance.

"The Irish setter is a breed characterized by a dark red color. Most individuals are dominant red, ABE, potentially black, but the black is hidden by the A gene." However some families probably include recessive reds without the A factor, i.e. *aaBee* in constitution. In mixed families a cross between dominant and recessive individuals might result, as it actually does, in the production of an occasional black pup.

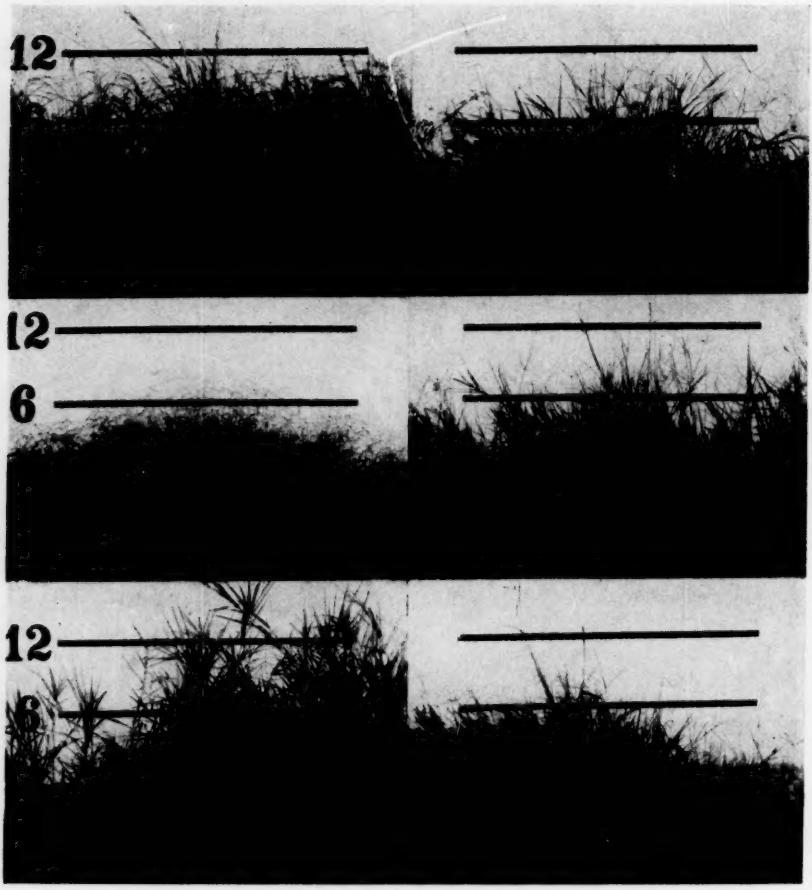
F_1 in such cases would be red ($AeBBEe$), but F_2 would produce genotypes $ABE(9)$: $ABee(3)$: $aaBE(3)$: $aaBee(1)$. The first two of these would be dominant red, since they contain A, the last recessive red, the third, black. The apparent inheritance ratio would thus be 13 red : 3 black.

Winge rather expects classes 2 and 4 to have brown noses but is not sure of it. His uncertainty results from the fact that he here assigns a wrong significance to gene B, regarding it as a "factor for red" rather than black, while "$B + E$ stands for black by compensatory action." In reality, B, in whatever combination, results in the production of black pigment. E governs its distribution in the coat. The combination BE does, as he states, produce a black coat, but Bee produces black restricted to eyes and skin, including nose.

Whenever B is replaced by *bb*, brown pigment replaces black in coat, eyes and skin, including nose.

This relationship is correctly shown in the genetic formulae of the excellent colored plates. It is unfortunate that in the descriptive text the author is not equally clear and consistent.

W. E. Castle
University of California, Berkeley.



BERMUDA GRASS—SPECIES AND HYBRIDS

Figure 12

Two important strains of Bermuda grass are coastal Bermuda (*A*), usually grown in the Southeastern states, and a cold-resistant strain, Indian Bermuda, which pushes the range of this useful pasture grass into the eastern corn belt. A related species, star grass (*C*) has recently been introduced from South Africa. It is a ranker growing grass than Bermuda. Hybrids of it with Indian Bermuda (*D-F*) are intermediate in size and other qualities. Some of these hybrids offer considerable promise as forage grasses.

INTRA- AND INTER-SPECIFIC HYBRIDS IN BERMUDA GRASS*

GLENN W. BURTON†

BERMUDA grass, *Cynodon dactylon* (L.) Pers. is one of the most important pasture grasses in the southeastern United States. Livestock men have long recognized its merits and many of them have used it as the main species in their improved pastures. The work with this species that led to the development of Coastal Bermuda[1] showed that it is highly cross-pollinated and that occasional intra-specific hybrids carry a great deal of hybrid vigor.[2] Coastal Bermuda, perhaps the best of these hybrids, has been superior to common Bermuda throughout most of the Bermuda Belt and is replacing common Bermuda for pastures and hay as rapidly as planting stock can be made available. In the northern part of the Belt, however, Coastal Bermuda has winterkilled more than the local strains of this grass, indicating that improved varieties for that area must carry more cold resistance than Coastal Bermuda. The desire to explore the possibilities of improving Coastal Bermuda through intra- or inter-specific hybridization led to the studies described here.

Materials and Methods

In the summer of 1942 attempts were made to produce controlled hybrids in all possible combinations of the following three Bermudas: Coastal Bermuda, Indiana Bermuda (both *C. dactylon*), and Star grass, *C. plectostachyum* (Schum.) Pilger. Coastal Bermuda, an intra-specific hybrid carrying a great deal of hybrid vigor, differs from common Bermuda in that it has much longer leaves, stems, and stolons and produces very few heads that rarely contain viable seed. (See Figure 12*A*.) It is highly resistant to the leaf spots caused by *Helminthosporium giganteum* and *H. cynodontis*, and is more resistant to frost and drought than the common Bermudas with which it has been compared.

Indiana Bermuda, a selection of common Bermuda that has survived the winter for many years at Lafayette, Indiana, was chosen as the cold resistant parent. (Coastal Bermuda winterkills completely at Lafayette.) This Bermuda, supplied by Dr. G. O. Mott of Purdue University, is similar to common Bermuda in growth habit (see Figure 12*B*), is much more susceptible to the *Helminthosporium* leaf spots, and is less frost resistant but more cold resistant than Coastal Bermuda.

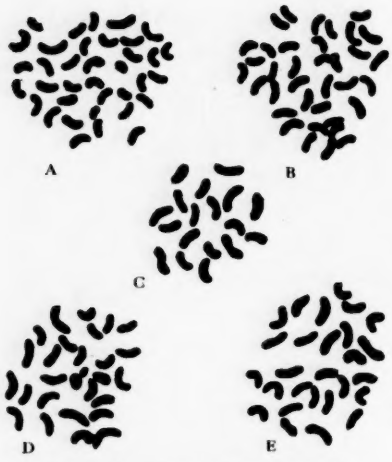
Star grass, *C. plectostachyum* (introduction P.I. 142280 from South Africa), is much taller, and has coarser stems, larger leaves, and longer internodes than either common or Coastal Bermuda grass. (See Figure 12*C*.) It spreads much faster than the common Bermudas and appears to be much more productive. The representatives of this species planted at Tifton have been quite susceptible to the *Helminthosporium* leaf spots, have winterkilled very badly (many of them completely), and have carried high concentrations of prussic acid.

Coastal and Indiana Bermuda were easily hybridized when the Indiana Bermuda was used as the female parent and enough seeds were produced to give rise to 66 F_1 hybrid plants. The Indiana Bermuda × Star grass cross was more difficult to make but 11 F_1 hybrid plants were obtained. Only three F_1 hybrids of the Coastal Bermuda × Star grass cross could be made and one of these died after it was transplanted to the field. On April 23, 1943, these F_1 plants and several clonal plants of each parent were spaced eight feet apart in each direction in the field. Representative plants of each cross are shown in Figure 12*D-F*. Studies of these hybrid plants in the summer of 1943 included comparisons of their gross morphology, fertility, and disease resistance. Somatic chromosomes in a number of the plants were counted using techniques previously described.[3] Prussic acid analyses were made of a number of the hybrids and parent plants using the technique described by Nowosad and MacVicar.[4]

A more accurate measure of the relative yield performance and morphology of some of

*Cooperative investigations at Tifton, Georgia, of the Division of Forage Crops and Diseases, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, The Georgia Coastal Plain Experiment Station, and the Georgia Experiment Station.

†Principal Geneticist, U. S. Department of Agriculture, Tifton, Georgia.



BERMUDA GRASS CHROMOSOMES
Figure 13

Somatic chromosomes of root metaphase plates in the *Cynodon* species parents and two of their hybrids. *A*—Coastal Bermuda (*C. dactylon*) $2n = 36$. *B*—Indiana Bermuda (*C. dactylon*) $2n = 36$. *C*—Star grass (*C. plectostachyum*) $2n = 18$. *D*—Coastal Bermuda × Star grass $2n = 27 + 1f$. *E*—Indiana Bermuda × Star grass, $2n = 27$.

these hybrids and their parents was provided by a test begun in the spring of 1944. Six-inch square blocks of sod of each of the bermudas listed in Table I were planted in the center of 4 × 24 foot plots in triplicate. The test was located on a Tifton sandy loam that had been planted to velvet bean cover crops for several years. Spring applications of 500 pounds per acre of 4-12-4 were made each year that records were taken. All measurements were subjected to statistical analysis.

Results

Intra-Specific Hybrids

All of the Indiana × Coastal Bermuda F_1 hybrids produced in this study carried the marks of both parents. The measurements in Table I show that they approached their more vigorous parent in rate of spread (plot length), plant height, and stem length. Many of them actually exceeded both parents in leaf width. All hybrids were more resistant to the *Helminthosporium* leaf spots than the Indiana Bermuda but none carried as much resistance as the Coastal parent.

The five hybrids compared in the yield test yielded slightly less than the average of the parents and the most productive of these plants did not yield significantly more than this average. (See Table I.) Thus, there was little evidence of heterosis in the expression of yield in these hybrids. They also maintained an intermediate position in percent cover (sod density).

The most productive of these hybrids, No. 13, was sent to Dr. G. O. Mott at Lafayette, Indiana, who planted it in the field with the two parents in the spring of 1944. This hybrid and the Indiana parent are still alive in this planting, whereas the Coastal parent winter-killed completely during the first winter. These results suggest that the genes for cold resistance in the Indiana Bermuda are largely dominant.

Several reports from the northern fringe of the Bermuda Grass Belt indicate that the Indiana × Coastal Bermuda hybrid No. 13 is more productive than the common types of Bermuda grass growing there. It seems quite probable, therefore, that this hybrid may assume economic importance in that region where the more productive Coastal Bermuda cannot be used, due to winter injury.

Inter-Specific Hybrids

The 13 plants obtained from the *C. dactylon* × *C. plectostachyum* crosses were considerably different from their female parents in gross morphology, indicating they probably were hybrids. This was particularly true of the Indiana Bermuda × Star grass plants. These plants spread faster, grew taller, and had much longer stems than the Indiana Bermuda. All of them exceeded their female parents in leaf width.

All of the inter-specific hybrids produced heads during the first growing season. These heads flowered normally but produced only tiny yellow anthers that failed to dehisce and contained only an occasional irregular sized pollen grain. All of the hybrids appeared to be completely sterile as was evidenced by the complete absence of caryopses in the florets examined.

Cytological studies of the mitotic figures in root tips of a number of *Cynodon dactylon* selections have revealed that this species probably carries 36 somatic chromosomes and often several chromosome fragments.[3] Similar studies made with the parents used in these crosses gave somatic counts ranging from 36 to 37 for Coastal Bermuda, 36 to 38 for Indiana Bermuda, and 18 to 19 for Star grass. These variations resulted in part from the difficulty of separating the

many chromosomes, some of which varied considerably in size. In some instances the extra "chromosomes" were so small as to be considered fragments. Usually, the best mitotic figures gave the lowest numbers suggesting that 18 and 36 were the chromosome numbers for the parents used in these studies. Somatic chromosome counts were made in the root tips of nine of the 13 interspecific hybrids. Although occasional figures (like the parents) showed one to several extra chromosomes or fragments, the preponderance of evidence pointed to 27 as the somatic chromosome number for each of these hybrids. Representative mitotic figures of the parents and hybrids are shown in Figure 13.

Repeated tests of the actively growing green shoots of Star grass have shown that they contain over 300 p.p.m. of prussic acid. Under the proper circumstances, such concentrations of this poison could kill the animals consuming the grass. *Cynodon dactylon* has never been found to carry any prussic acid. The prussic acid test[4] was applied to the parents and inter-specific hybrids during the summer of 1943 with the following results: Two of the Indiana Bermuda × Star grass hybrids contained about 100 p.p.m. of prussic acid, four showed a trace of the poison, and five gave no reaction, indicating they were free of prussic acid. One of the Coastal Bermuda × Star grass hybrids contained about 75 p.p.m. of prussic acid, whereas the other contained none. Both Coastal and Indiana Bermuda gave a negative reaction to the test but Star grasses gave a strong positive reaction, indicating the presence of more than 300 p.p.m. of prussic acid. These results suggest that "no prussic acid" tends to be dominant over "high prussic acid" or that the genes controlling high prussic acid in the Star grass parent were in a heterozygous condition.

Star grass winterkilled badly during the winter of 1944-1945 and maintained a very poor stand during the next two summers. It disappeared completely from the test plots following the winter of 1947-1948, with minimum January temperatures of 16 degrees above zero (Fahrenheit). The *C. dactylon* parents and all of the inter-specific hybrids came through these temperatures in good condition.

Since Star grass winterkilled badly in the winter of 1944-1945 and maintained less than a 25 percent stand thereafter, only the 1944 yields can be taken as an index of its yield capacity. The average 1944 yields of the six Indiana Bermuda × Star grass hybrids included in the yield test (Table I) approached the yield of Star grass, their most productive parent. The best of these hybrids actually produced significantly more forage than Star grass, demonstrating the existence of considerable heterosis. Table I shows that the two Coastal Bermuda × Star grass hybrids were significantly different in yields and percent cover throughout the test. Hybrid No. 4-30, the most productive of these hybrids, yielded significantly less than the average of its two parents in 1944 but

TABLE I. The Comparative Performance of Intra- and Inter-Specific Bermuda Grass Hybrids Grown at Tifton, Georgia.

Bermuda Grasses Tested	Plot Length in Inches 6-15-44	Plot Length in Inches 11-7-44	Plant Height in Inches 11-7-44	Stem Length in Inches 11-7-44	Yield of Dry Matter Pounds Per Acre 1944	1945	1946	Percent Cover 1946
Indiana Bermuda (*C. dactylon*)	40	64	7	12	3,430	1,200	2,710	70
Coastal Bermuda (*C. dactylon*)	80	256	14	31	11,480	4,400	4,293	93
Average of 5 Indiana × Coastal F_1 hybrids	96	248	13	25	6,692	2,720	2,513	84
The most productive Indiana × Coastal F_1 hybrid No. 13	104	256	14	22	8,820	3,400	2,907	90
Star Bermuda (*C. plectostachyum*)	80	392	20	31	5,530	1,100	1,023	22
Average of 6 Indiana × Star F_1 hybrids	104	248	13	21	5,390	2,370	2,180	68
The most productive Indiana × Star F_1 hybrids	96	240	17	24	7,140	3,500	2,803	90
Coastal × Star F_1 No. 4-30	120	344	12	28	7,000	4,000	4,067	90
Coastal × Star F_1 No. 6-30	104	272	15	27	5,250	2,300	2,793	57
5% L.S.D.	26	74	3.9	6.2	2,870	648	547	28
5% L.S.D. between averages 5 and 6	11	30	1.6	2.5	1,169	276	164	11

approached the yield of its Coastal Bermuda parent in the last two years of the test.

Summary and Conclusions

Coastal Bermuda grass (an unusually productive intra-specific, *C. dactylon* hybrid), a cold resistant *C. dactylon* from Indiana, and Star grass, *C. plectostachyum*, were crossed in all possible combinations in the summer of 1942. Sixty-six Indiana × Coastal Bermuda hybrids, 11 Indiana Bermuda × Star grass hybrids, and three Coastal Bermuda × Star grass hybrids were made. None of these hybrids were as productive as Coastal Bermuda.

Intra-specific hybrids between Indiana Bermuda and Coastal Bermuda were intermediate in all characters measured. One of these hybrids, considerably more productive than its Indiana parent, has survived the winters at Lafayette, Indiana, where Coastal Bermuda has winterkilled completely, suggesting that the genes for cold resistance are largely dominant. Early tests indicate that this hybrid may assume economic importance in the northern part of the Bermuda Grass Belt where the more productive Coastal Bermuda winterkills.

The 13 inter-specific hybrids flowered but were completely sterile. Cytological studies showed all of them to be triploids ($2n = 27$). Both *C. dactylon* parents possessed 36 somatic chromosomes, whereas *C. plectostachyum* contained 18 somatic chromosomes. Chromosome fragments, occasionally approaching chromosome size, were observed in some figures. Prussic acid analyses of green shoots showed the *C. dactylon* parents to be free, Star grass to contain 300 p.p.m., two hybrids to contain 100 p.p.m., one to contain 75 p.p.m., four to contain a trace, and six to be free of this poison. Star grass winterkilled completely during a winter with minimum temperatures of 16 degrees above zero (Fahrenheit). The *C. dactylon* parents and all of the inter-specific hybrids came through this winter in good condition. The best of the Indiana Bermuda × Star grass hybrids significantly outyielded its most productive parent, demonstrating the existence of heterosis.

The significant differences in yield performance between hybrids involving the same parents was to be expected. All gamates from such heterozygous parents could not be expected to combine equally well. These variation in yield suggest that hybrids, better than any of those tested, might have been found, had a greater number of them been available for testing. The limited data from these studies indicate intra-specific hybridization is more effective than inter-specific hybridization (with *C. plectostochyum*) in the improvement of *C. dactylon*.

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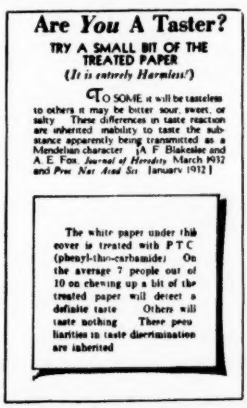
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